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RELATIVE PERFORMANCE OF WASHINGTON NAVEL ORANGE SELECTIONS AND OTHER NAVEL VARIETIES

By RAIMUND H. MARLOTH and W. J. BASSON
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THE Washington Navel orange group is one of the most widely grown commercial citrus fruits in the world. Of the 130 million cases of oranges produced in the United States some 20 million are navels. In Spain 37 per cent. of an acreage capable of producing 40 million cases of oranges is planted to navels and in South Africa the proportion is similar. The navel tree performs best under climatic conditions that are moderately warm during the growing season but with a distinct cold spell during the winter. Thus it is found that navels in South Africa yield higher and have better quality fruit in the Rustenburg and the Kat River areas than in the Lowveld proper.

The Washington Navel orange, as known to the world to-day, is accepted as having originated at Bahia, Brazil, in the early part of the nineteenth century as a bud sport or mutation from the Selecta or common seeded variety. That it must be regarded as a rather " unstable " group is amply demonstrated in the numerous publications of the late A. D. Shamel and his associates. Even though only two parent trees of the Washington Navel orange had been introduced into California in 1873, already some forty years later Shamel, Pomeroy and Caryl (1929) could report on the yield and fruit quality of nineteen widely cultivated strains and five of minor economic consequence, all of which had been obtained from commercial orchards. Apart from undesirable variants, Webber and Batchelor (1946) list sixteen named varieties in the navel fruit group, which number has been added to considerably since then.

Materials and methods.

Some twenty varieties and selections of navel oranges, gathered from all over South Africa, had been under observation at the Citrus and Subtropical Horticultural Research Station, Nelspruit, in the Eastern Transvaal from 1930 onwards. Seven of these were selected for comparative plantings in two different climatic areas, in the eastern Transvaal and Eastern Cape Province. The selections included strains of the true Washington Navel variety, of which old established parent orchards had been the source of much budwood used in the propagation of trees in many South African orchards. For these selected strains, claims had been advanced for superior tree performance and fruit quality, some of which had been substantiated in preliminary studies. Four strains of Washington Navel were included, viz. Greathead, Knight, Pickstone and Flannagan; the remaining three were apparently distinct navel varieties, Company, Pretoria and Robertson.

Sister-trees on rough lemon rootstocks were propagated for both plantings, the seed for the rootstocks coming from one mother tree and the budwood for each strain from one parent tree of known history. For the Eastern Transvaal two selections, Greathead and Pretoria Navel, were also propagated on sweet orange rootstocks.

The resultant trees were planted in 1941 on a red sandy loam soil at the Alkmaar Substation in the Eastern Transvaal and on a heavy black alluvial clay loam at Baddaford, near Fort Beaufort, in the Kat River Valley. The climates of the two areas are quite different, the former having a mild winter and summer rainfall, while the latter is often subject to fruit-damaging frosts in winter and its variable lower rainfall is distributed throughout the year.

The layout of both plantings was in randomized blocks, with two-tree plots, each replicated four times.

Growth, yield, and fruit quality data were recorded at Alkmaar over the seventeen years from planting and at Baddaford for the eight-year period 1949-57. All data were subjected to statistical analysis.

Growth was determined by trunk measurements and by estimations of relative tree size. Annual yield was recorded by weighing and counting the fruits from each tree. For fruit quality, samples of 20 similar-sized fruits were taken from each two-tree plot. Unless otherwise stated, results commented on are from the Alkmaar planting.

RESULTS.

Growth.

Although budded to sister-stocks, already at planting the trees of Robertson Navel and the Pickstone strain of Washington Navel were definitely smaller in trunk diameter, at two inches above the union, than trees of the other selections. With Robertson Navel even the rootstock had been retarded in growth, giving a smaller diameter two inches below the union than did all the other selections. There was no significant difference in size between budlings of the two selections on rough lemon and sweet orange rootstocks.

At 17 years old at Alkmaar, trees of Robertson Navel were significantly the smallest of all (Fig. 1). The trunk diameters of trees of the Company and Pretoria Navels were much greater than those of all other selections. Pretoria Navel and the Greathead strain on sweet orange rootstock were now significantly larger than trees on rough lemon.

As they became older, trees of the Greathead strain on rough lemon rootstock were smaller than comparable trees of the other three strains of the true Washington Navel orange. Olsen *et al.* (1957) were the first to show that trees affected with exocortis or xyloporosis virus when grown on a virus-sensitive rootstock were smaller than apparently healthy trees. McClean *et al.* (1958) showed that the Greathead strain carried the exocortis virus. As shown by its reaction on sweet lime rootstock in other plantings at Nelspruit, the Greathead navel also carries the xyloporosis virus. Whether the smaller tree size on rough lemon, which rootstock has hitherto been regarded as resistant to the two viruses, is an inherent characteristic of the strain, or whether it results from the presence of virus cannot be decided until a comparison can be made with nucellar material free of known bud-transmissible viruses (i.e. other than tristeza which is insect-transmitted).

Yield per tree.

The yields for the Alkmaar planting are presented in Table I, and those for Baddaford in Table II.

The Robertson Navel gave the lowest yield per tree over the whole period, much less than any of the four Washington Navel strains and, from 1953 to 1957, also less than the Pretoria and Company Navels. At Alkmaar both the latter varieties consistently yielded less than the true Washington Navels. There was no significant difference in yield in any period between trees of the Greathead strain and Pretoria Navel on rough lemon rootstocks and those on sweet orange.

Since the trees at Baddaford are sister-trees of those at Alkmaar, it might be expected that their yield pattern would be similar. However, there was no clear-cut difference in weight of fruit per tree between selections at any period (Table II). It is noteworthy that the average weight of fruit produced per tree at Baddaford was higher for all selections than at Alkmaar, viz. 171 lb. as against 135 lb. per tree per year over the eight-year period 1949-57. This difference in performance may be ascribed to a more favourable climate for the navel in the Kat River Valley than at Alkmaar.

Fruit size.

The differences in weight per fruit are so well defined and consistent that they probably reflect distinct differences in actual fruit size.

Fruits of the Robertson Navel were the smallest and the Company and Pretoria Navel fruits were definitely smaller than those of the four Washington Navel strains. Within these strains there was no distinct difference. As shown by Tables I and II the fruit from Baddaford was smaller than that from Alkmaar.

Table I shows that the fruit from all selections definitely decreased in weight as the trees got older. This also occurred at Baddaford. With grapefruit, Marloth (1958) ascribed this decrease in fruit size solely to the deteriorating effects on the tree of the " stem-pitting " virus. The evidence now offered seems to show that this progressive decrease in size for at least the first seventeen years of the tree's life is a natural physiological occurrence with increasing age, quite apart from any possible effects of other factors. The average fruit size of all selections during their first four years of bearing was equivalent to a pack-size of 126 fruits per standard export case; in the next four years of bearing it was 150, and, in the last period, 176.

Fruit quality.

In comparing fruit quality factors of the various selections it must be borne in mind that each determination for a single planting was made on a given date. That the relative values would sometimes have differed before or after that date is shown by determinations made over years with fruit from the same selections from other plantings. The fruit quality factors which for practical purposes are mainly affected by the time of testing are total soluble solids and acid content, with consequent changes in ratio.

Rind thickness. At Alkmaar the rinds of the fruits of the Robertson, Company, and Pretoria Navels were much thinner than those of the four Washington Navels. Fruits of the two selections on sweet orange rootstock had thinner rinds than on rough lemon. All seven selections at Baddaford had markedly thinner rinds than

TABLE I.

Yield and fruit quality of seven navel strains at Alkmaar.

Strain	Average yearly yield in lb. per tree				Average weight per fruit in lb. (fruit size)				Fruit quality, average for 10 years				
	1945-48 4 yrs.	1949-52 4 yrs.	1953-57 4 yrs.*	1945-57 12 yrs.	1945-48 4 yrs.	1949-52 4 yrs.	1953-57 4 yrs.*	1945-57 12 yrs.	Rind thickness cm.	% Juice	% Total soluble solids	% Acid	T.S.S./acid ratio
On rough lemon rootstock													
W. Navel (Greathead) ..	30	130	163	108	0·59	0·53	0·49	0·53	0·60	45·3	9·6	0·84	11·5
W. Navel (Knight)	38	139	182	120	0·62	0·52	0·49	0·54	0·63	44·4	9·7	0·85	11·4
W. Navel (Pickstone) ..	36	123	159	106	0·61	0·50	0·47	0·53	0·60	44·6	9·5	0·90	11·2
W. Navel (Flannagan) ..	33	116	166	105	0·64	0·52	0·50	0·55	0·60	44·6	9·8	0·89	11·0
Company Navel	20	90	152	87	0·55	0·45	0·42	0·47	0·57	50·9	8·8	1·17	7·6
Pretoria Navel	14	70	195	93	0·53	0·49	0·43	0·49	0·57	50·9	9·0	1·21	7·5
Robertson Navel	25	91	109	75	0·50	0·45	0·34	0·43	0·56	44·1	10·3	0·83	12·7
Average	*28*	*108*	*161*	*99*	*0·58*	*0·49*	*0·45*	*0·51*	*0·59*	*46·4*	*9·5*	*0·96*	*10·4*
On sweet orange rootstock													
W. Navel (Greathead) ..	32	134	207	124	0·54	0·54	0·48	0·52	0·55	47·2	10·1	0·92	11·1
Pretoria Navel	21	76	138	78	0·52	0·46	0·43	0·47	0·52	52·1	9·6	1·29	7·6
Sig. diff. P=0·01	n.s.	29	48	22	0·07	0·05	0·04	0·04	0·03	1·9	0·63	0·06	1·4
P=0·05	16	22	35	17	0·05	0·04	0·03	0·03	0·02	1·4	0·46	0·04	1·1

* No crop in 1955 as result of hailstorm.

TABLE II.

Yield and fruit quality of seven navel strains on rough lemon rootstock at Baddaford.

Strain	Av. yearly wt. of fruit in lb. per tree			Av. no. of fruits per tree	Av. wt. of fruit in lb.	Fruit quality Av. for six years				
	1949-54 5 yrs.	1955-57 3 yrs.	Av. 8 yrs.			Rind thickness in cm.	% Juice	% Total soluble solids	% Acid	T.S.S./ acid ratio
W. Navel (Greathead) ..	113	223	168	377	0·45	0·53	47·7	10·2	0·84	12·3
W. Navel (Knight)	130	231	181	408	0·44	0·53	45·6	10·4	0·90	11·8
W. Navel (Pickstone) ..	117	219	168	390	0·43	0·52	45·3	10·3	0·85	12·2
W. Navel (Flannagan) ..	134	224	179	420	0·43	0·52	45·9	10·6	0·87	12·2
Company Navel	164	286	225	602	0·37	0·49	51·5	10·3	1·15	9·1
Pretoria Navel	124	227	176	503	0·35	0·47	52·2	10·2	1·12	9·1
Robertson Navel*	85	115	100	258	0·39	0·48	47·8	10·4	0·84	12·9
Average	*124*	*218*	*171*	*423*	*0·41*	*0·50*	*48·0*	*10·3*	*0·94*	*11·4*
Sig. diff. P=0·01	n.s.	122	n.s.	245	0·05	0·04	3·0	n.s.	0·07	0·7
P=0·05	n.s.	90	n.s.	179	0·03	0·03	2·2	n.s.	0·05	0·5

* Trees cut for budwood from 1955 onwards, therefore significance for yield not computed.

at Alkmaar; this difference is probably connected with climate. The differences between the selections at Baddaford in general follow the same lines as those at Alkmaar.

A study of the yearly measurements over the first twelve years of bearing shows that with all seven selections the rind thickness steadily decreased, the averages for all on both rootstocks in successive years of heavy cropping between 1946 and 1957 being 0·60, 0·59, 0·59, 0·57, 0·50, 0·54, 0·49 cm., each being the mean of 720 measurements of individual fruits of approximately the same pack-size. Although it is well known that citrus fruits from young trees have much thicker rinds than those from older trees, to the writers' knowledge evidence for this physiological fact has not been presented before.

Juice. The highest juice content was found in fruits of the Pretoria and Company Navels; both at Alkmaar and Baddaford these varieties had about 3 per cent. more juice, a highly significant difference.

At Alkmaar, fruits of both selections on sweet orange rootstocks had from 3 to 5 per cent. more juice than those from trees on rough lemon, the average difference of 3·3 per cent. being also highly significant.

Fruit grown at Baddaford had consistently more juice than had fruit of the same selection grown at Alkmaar, the overall average difference being 1·6 per cent.

Total soluble solids. At the end of May, the Robertson Navel fruits at Alkmaar, with an average of 10·3 per cent., invariably had more total soluble solids than those of all the other selections, which averaged only 9·4 per cent. Fruits of the Company and Pretoria Navels at that date were the lowest of all in total soluble solids.

At Baddaford, no real differences for total soluble solids of fruit were found in the six years' fruit tests made at the end of June.

Fruits from trees on rough lemon rootstock had less soluble solids throughout than those from trees on sweet orange, the respective average figures for the ten years being 9·3 and 9·9 per cent.

In the Baddaford planting fruits from all selections, tested at the end of June, showed a slightly but consistently higher total soluble solids content than did fruits from the sister-trees at Alkmaar tested a month earlier, the relative averages being 10·3 and 9·9 per cent. respectively. In the writers' view the higher total soluble solids content reached in the Baddaford planting may well be ascribed to a direct effect of climate.

Acid. At times of testing, in both plantings, the acid content of fruits of the Company and the Pretoria Navels, with over 1·1 per cent. acid in the juice, was definitely higher than that for the other five selections.

The acid content of the two selections (Greathead and Pretoria) on sweet orange rootstocks was higher than that on rough lemon throughout.

Ratio of total soluble solids to acid. The average T.S.S./acid ratios for all selections in the Alkmaar and Baddaford plantings were 10·4 and 11·4 respectively. In the Robertson Navel the ratios (12·7 and 12·9) were much higher. The consistently lower values for the Pretoria (7·6 and 9·1) and the Company (7·5 and 9·1) Navels were primarily due to the relatively high acid values for these two navels. These marked differences were consistent throughout the years of testing.

Seeds. Counts were made over five years of seeds in fruits of 17 of the original navel strains in different plantings. In all, over 300 tests were made using from 10 to 20 fruits per sample, and these showed only nine of these selections to be absolutely

seedless. The presence or absence of seeds was a definite characteristic of some varieties or strains. For example, one Bahia strain had an overall average of 1·6 seeds per fruit, whereas in another not a single seed was found. Both the Company and Pretoria Navels tended to have a seed or two in most of their fruits, and the Knight strain of Washington Navel averaged one seed in ten fruits. The other three Washington Navels and the Robertson Navel can be considered truly seedless.

Maturity.

Although area and climate may have a great influence, the characteristic of earliness or lateness of ripening is relatively constant for each variety, though expressed to a different degree.

The Greathead strain of Washington Navel may be regarded as typical of the varietal group in regard to time of ripening. The average values for certain fruit quality factors as determined over two years at Nelspruit in the Eastern Transvaal show that the Greathead Navel had for all practical purposes reached maturity at the end of April, seeing that by June the values for total soluble solids had increased from 10·1 to only 10·5 per cent., while the acid in the same period had decreased considerably, from 1·2 to 0·9 per cent. However, with both the Company and Pretoria Navels, while their total soluble solids in April were the same as that of the Greathead strain, by June the values had risen to 11·1 and 11·0 per cent. respectively.

As regards acid content the position was somewhat different. In April the Company and Pretoria Navels had acid values considerably higher than that of the Greathead Navel and this difference was still maintained in June. In other words, while the fruit of the Greathead Navel tended to become over-mature, that of the Company and Pretoria Navels has only then reached full maturity. Thus both the Company and Pretoria Navels must be regarded as late-maturing or late-ripening navel varieties.

Because of the significantly higher T.S.S./acid ratio for the Robertson Navel in both the Alkmaar and Baddaford plantings, and the appreciably higher value already reached in April at Nelspruit as compared with the ratios of the Washington Navel orange varieties, this variety must definitely be regarded as early-maturing. It is worth adding that fruit of the Robertson Navel also colours up several weeks earlier than that of the other selections.

DISCUSSION.

The disadvantages of an unduly large tree are constantly being referred to by citrus growers the world over, especially in these days of high wages and labour shortage, but only in Japan, through the use of dwarfing rootstocks, has the smaller citrus tree been grown generally in commerce. Thus the lower yield per tree of the Robertson Navel is in itself not a disadvantage, as the trees are distinctly smaller than those of the Washington Navel strains with higher yields. Trees of this or any similar " dwarfed " variety could be planted closer.

It is important to note that trees of both the Company and Pretoria Navels at Baddaford consistently bore crops equal to those of the four Washington Navel strains. If the results of the Alkmaar planting alone had been available, the Company and Pretoria Navel varieties would have appeared to be inherently lower yielding (an undesirable characteristic transmissible by propagation) than the four Washington

Navels. However, in view of the Baddaford results, it appears that under different climatic conditions this characteristic may not express itself, or may even show up in the reverse order. This aspect is well known for distinct types of varieties of citrus, but to the best of the writers' knowledge evidence as to its existence between members of a varietal group is lacking.

Citriculturists in all countries have become very " virus conscious ". As elsewhere, at Nelspruit work is in hand to produce bud-transmissible virus-free nucellar lines of the leading commercial varieties, and to test parent material already in use, both as rootstock and scion, for the presence of virus infection. The part played by the different viruses in influencing tree growth, longevity, production and fruit quality is not yet fully understood. Thus caution must be exercised in evaluating the performance of any given citrus variety or strain in case some features of it may be due not wholly to inherent characteristics or climatic influences but also to the, as yet undetermined, effects of the presence of a virus. The extension of the present investigation already started, besides indexing all material for virus content, aims at the comparative evaluation of performance and fruit quality of a relatively large number of commercial varieties and strains of navel oranges from other citrus-growing countries of the world, including some of nucellar origin.

SUMMARY.

Partly as the result of repeated introductions of trees from Brazil and California there exist to-day in most citrus-growing countries distinct navel orange varieties and strains in commercial orchards.

Results are reported of studies of the orchard growth, yield and fruit quality of three selected navel varieties and four Washington Navel strains at Alkmaar in the Eastern Transvaal and at Baddaford in Eastern Cape Province, over a period of 12 years at the former and 8 years at the latter.

In the nursery, budlings of Robertson and Pickstone Navels were smaller than the others. At 17 years old the Robertson trees were the smallest and Company and Pretoria trees the largest; the four strains of Washington Navel, which included Pickstone, did not differ in size.

The smaller Robertson Navel trees yielded less than the other selections; there was no difference in yield between the four strains of Washington Navel. Robertson bore the smallest fruit of all and the two other navel varieties had smaller fruit than the four Washington Navels, which did not differ.

Company and Pretoria Navels had thinner rinds, higher juice contents, less total soluble solids and more acid, and hence a lower T.S.S./acid ratio than the other selections. Robertson Navel had a thinner rind, sometimes more juice and consistently higher total soluble solids than the four Washington strains. The Robertson Navel matured early and the Company and Pretoria Navels late.

The presence of occasional seeds in the fruits was established as a characteristic of some navel varieties and strains.

At Alkmaar two of the selections yielded alike when worked on rough lemon and sweet orange rootstocks but on the latter the fruits had thinner rinds, more juice and higher total soluble solids, and were slightly more acid.

The average yield per tree was higher at Baddaford than at Alkmaar but the

PLATE I.

Fig. 1.

Left: Robertson Navel orange on rough lemon rootstock.
Right: Pretoria Navel on sweet orange rootstock.
Trees 17 years old, equidistant from camera—Alkmaar.

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fruit was smaller. At both Stations, as the trees grew older, there was a decrease in fruit size, a steady decrease in rind thickness and an increase in the total soluble solids content of the juice. The fruits from Baddaford had thinner rinds, more juice and higher total soluble solids content than those from Alkmaar.

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AUXINS IN PARTHENOCARPIC AND NON-PARTHENOCARPIC FIGS

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SYNOPSIS.

Studies of the auxin content of developing fig fruits revealed a sudden 30-fold increase in auxin concentration in the variety Calimyrna at the time of formation of the endosperm tissue. A similar and even larger rise in the parthenocarpic Mission variety was associated with the development of a parthenogenetic endosperm. By chromatographic analysis this auxin was shown to be different from those present at earlier and later stages of growth and to be chemically distinct from indoleacetic acid. Its function is thought to be the prevention of fruit drop. No evidence was found that the rate of fruit enlargement was in any way dependent on the auxin concentration.

In the fig (*Ficus carica* L.) growth of the fruit proceeds in three well-defined stages, two periods of rapid growth being separated by an intermediate period during which there is little or no increase in diameter (4). The double sigmoid growth curve characteristic of the fig is also shown by many drupaceous fruits (6, 21) and, to a less marked extent, by the black currant (22) and the blueberry (23). In the fig the general shape of the growth curve is similar in parthenocarpic varieties and in seeded varieties that will develop only following pollination.

By the application of the synthetic auxin 2,4,5-trichlorophenoxyacetic acid to figs at the end of their first phase of rapid development, the intermediate period of slow growth may be eliminated and the fruits brought to maturity as much as 60 days earlier than untreated controls (2). This suggested to Crane and Blondeau (5) that the period of slow growth might be associated with a low level of native auxin in the fruit at this stage, and the primary objective of the present study was to determine whether any such relationship existed between the growth rate of the fruit and its auxin content. A secondary objective was to compare, both quantitatively and qualitatively, the seasonal changes in auxin in the fruits of parthenocarpic and non-parthenocarpic varieties of fig.

The fig varieties used in this work were Mission and Calimyrna. Mission is completely parthenocarpic, fruits being produced in the absence of pollination and fertilization, whereas in Calimyrna fruit development is dependent on the process of caprification (pollination). The trees utilized were in adjacent commercial orchards at Merced, California, and were growing under identical environmental and cultural conditions, except that the Mission orchard was not caprified.

* Senior Postdoctoral Fellow, National Science Foundation, 1957-58.

Experimental methods.

Collection of material.

Fruit samples for auxin analysis were taken at approximately weekly intervals from 24th May to 15th August, 1957. At each sampling 50 or more of the figs nearest the base of the current season's shoots were picked, immediately cut into small pieces and frozen in dry ice for transport to the laboratory at Davis, where they were held at —10° C. The samples were then freeze-dried, ground in a Wiley mill to pass a 20-mesh screen, and packed in moisture-proof bags for air shipment to England, where the auxin analyses were subsequently made.

Growth measurements.

Five figs nearest the base of the current season's shoots of each of five trees of each variety were tagged and diameter measurements of each of the 50 fruits were made with vernier calipers at approximately weekly intervals. The resulting growth curves have been plotted in Fig. 1. Fruits in this position are initiated at the same time and show exceptionally uniform growth, the largest standard deviation found being 4·5 mm. for the sample of mature Calimyrna figs of mean diameter 52 mm.

Seed development.

For microscopic studies fruits were collected twice a week from 6th June to 28th July. Transverse segments ½ inch thick were removed from the regions of greatest diameter, fixed in Randolph's solution and embedded in paraffin for subsequent sectioning and staining.

Auxin extraction.

Prior to extraction the freeze-dried samples were stored in a cold room at 4° C. for periods which varied from 3 to 9 months. After preliminary trials of various methods of auxin extraction the following procedure, designed to extract the bulk of the " free " auxin from the tissue, was adopted:

To 10 gm. of the ground freeze-dried material was added sufficient phosphate buffer of pH 4·0 to saturate it (about 35 ml.). The wet powder was then shaken for 5 minutes with 100 ml. of buffer-saturated ether (" anaesthetic " grade) and allowed to stand. The ether was decanted and the extraction repeated with three further 100 ml. portions of ether. The bulked ether extracts were distilled to 25 ml. and passed through a column of activated alumina (90 × 12 mm.) on which the acidic constituents were adsorbed (10). The column was washed with 30 ml. dry ether and dried by drawing air through it for several minutes. The dry column was then eluted with 15 ml. of 2 per cent. sodium bicarbonate solution followed by 10 ml. distilled water. Three drops of methyl orange were added and the eluate titrated against N/10 HCl until the pH reached 3·0, as estimated by indicator paper. The acidified solution was then partitioned four times with 50 ml. of ether. The ether was dehydrated by leaving it for some hours at —10° C. and was drip-distilled to dryness in a small test tube. The final extract was taken up in 0·2 ml. ethanol for spotting on the chromatogram paper.

Any neutral auxins present in the original material would be expected to pass through the alumina column in ether solution, together with chlorophyll and fatty

materials. This fraction was accordingly taken to dryness and dissolved in 40 ml. hexane which was then partitioned twice with 50 ml. portions of acetonitrile (18). The acetonitrile was taken off under reduced pressure and the residue digested with 20 ml. distilled water. The water solution was then partitioned three times with 40 ml. ether which, after dehydration by freezing, was distilled to dryness and taken up in 0·2 ml. ethanol as for the acid fraction.

Paper chromatography.

All extracts were chromatographed on Whatman No. 1 paper using as a solvent a mixture of iso-propanol, 10; water, 1; ammonia, 1 (19). Several parallel chromatograms of each extract were run. Some of these were examined under ultra-violet light to locate fluorescent compounds and subsequently treated with Salkowski reagent to detect indole derivatives; others were subjected to bioassay to locate auxins and growth inhibitors. Control spots with indoleacetic acid and sometimes with indoleacetonitrile as well were run with each chromatogram.

Bioassay of auxins.

In the early stages of the work chromatograms were assayed for auxin activity by the wheat coleoptile cylinder test (14, 22) and the *Coleus* petiole abscission test (16). The general auxin pattern revealed by these tests was the same, but in the coleoptile test the auxin peaks were often partially obscured by growth-inhibiting substances which prevented accurate quantitative assessment. Hence, in the later stages of the work, only the *Coleus* test, which is relatively insensitive to inhibitors, was used. This test also has the advantage of being more specific for auxins than the coleoptile cylinder test, in which significant increases in growth may be given by substances (e.g. sugars, chelating agents) of quite unrelated structure. No substances other than auxins, however, have yet been found which show activity in delaying abscission in excised petioles; neither have any auxins yet been found which are not active to some extent in the *Coleus* test. Hence there seems little doubt that the substances assayed in these experiments are in fact auxins within the generally accepted meaning of the term.

The chromatogram strips were cut into 42 portions which were applied directly to the *Coleus* petioles as described in a previous paper (16), and the number of days to abscission measured. Estimates of the total auxin present in each extract in terms of indoleacetic acid equivalents were made by using a previously constructed calibration curve relating days delay in abscission to μg. indoleacetic acid per petiole.

RESULTS.

Changes in total auxin.

The concentration of total free auxin in the fruits of both fig varieties, as estimated from bioassay of the chromatograms, fluctuated within wide limits during the course of the growing season. For this reason auxin concentrations in Fig. 1 have been plotted on a logarithmic rather than on an arithmetic scale.

In both Calimyrna and Mission the concentration of auxin in the fruits during stage I, a period of rapid increase in diameter, was relatively low. Caprification of the non-parthenocarpic Calimyrna variety occurred towards the end of this stage

and shortly afterwards, on 21st June, when only caprified fruits were sampled, a sudden 30-fold increase in auxin concentration was found. A similar but even larger increase, of the order of 350 times, occurred at the same time in the parthenocarpic Mission figs, in which no caprification had taken place. In these the auxin concentration reached the exceptionally high value of 35 mg. equivalents indoleacetic acid per kg. dry weight of plant material. These very high auxin levels were maintained only for a short time and by the following week the auxin concentration in both

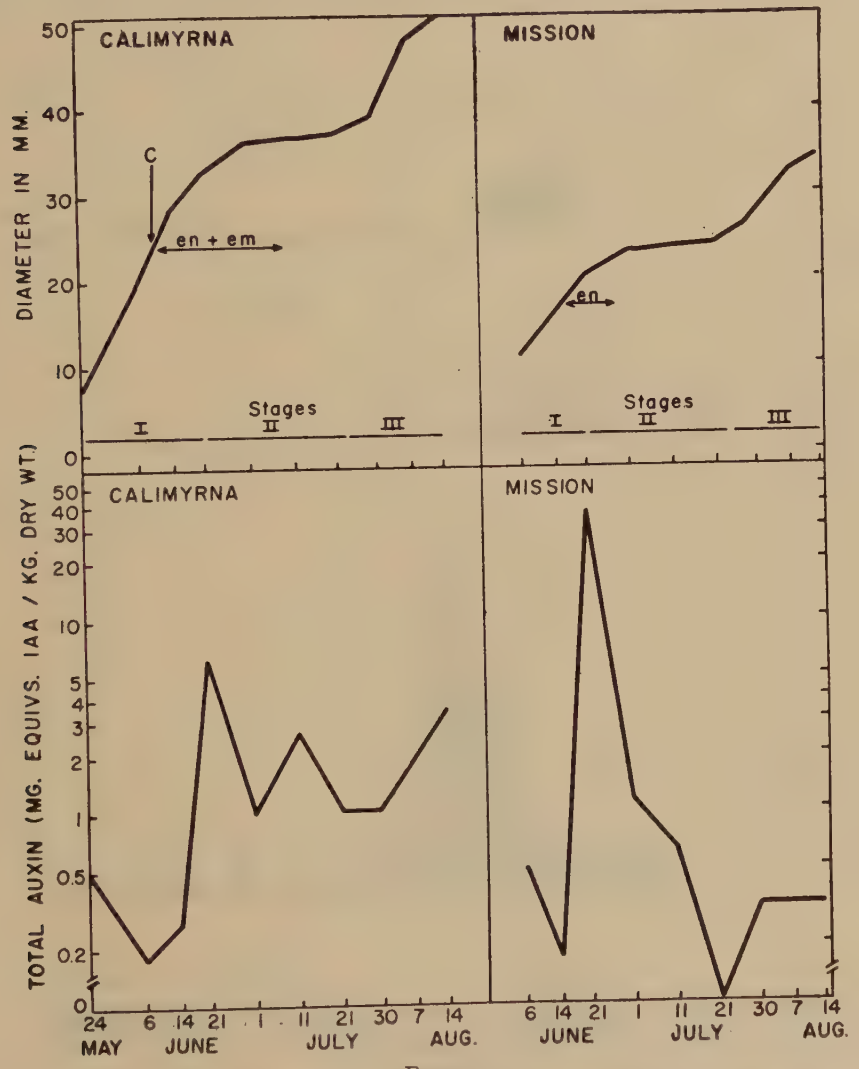

FIG. 1.

Above: Growth curves of Calimyrna and Mission fig fruits. C, caprification; en, em, period of endosperm and embryo development respectively.

Below: Changes in concentration of total "free" auxin in Calimyrna and Mission fig fruits throughout the season.

varieties had fallen to approximately 1 mg./kg. Subsequently, the auxin concentration in Mission continued to fall, whereas that in Calimyrna was maintained at between 1 and 3 mg./kg. throughout stages II and III.

Qualitative changes in auxin.

In Fig. 2 are shown typical chromatograms, bioassayed in the *Coleus* abscission test, of extracts of Calimyrna fig syconia at different stages of development. Essentially similar chromatograms were obtained from extracts of Mission figs. All the

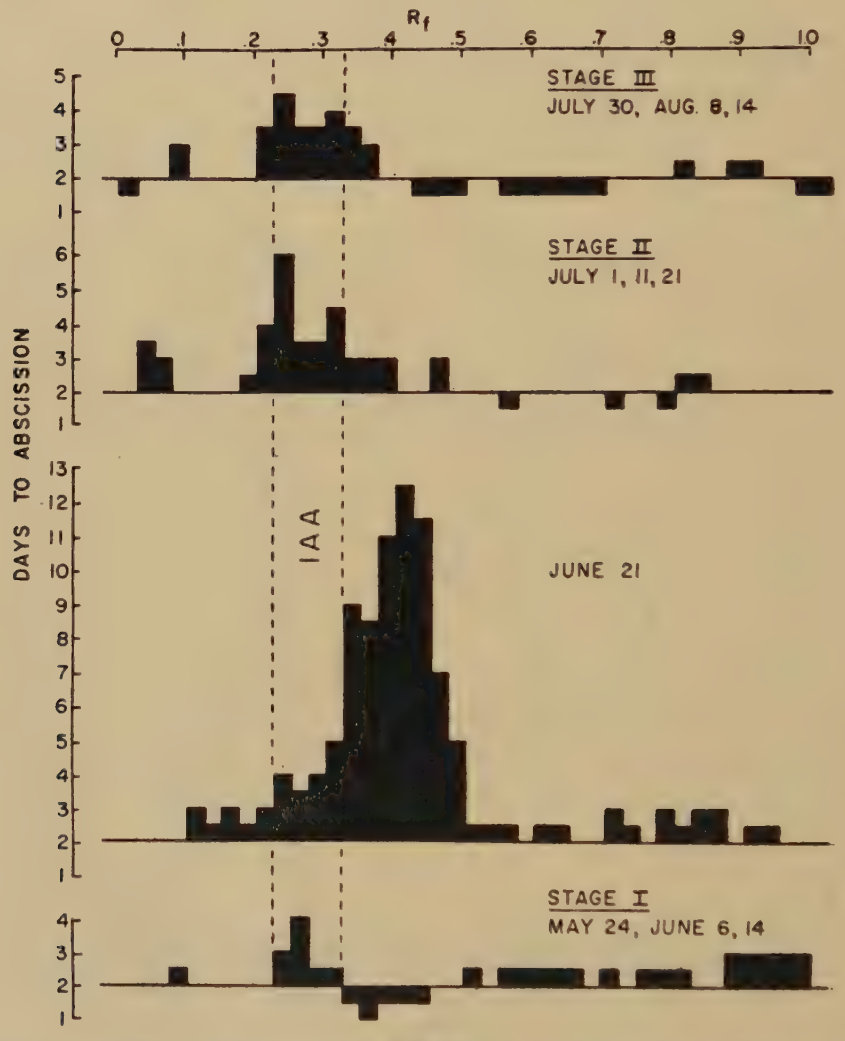

Fig. 2.

Typical chromatograms of ether extracts of Calimyrna fig fruits at different stages of growth, bioassayed in the *Coleus* petiole abscission test. All chromatograms were loaded with an amount of extract equivalent to 1·5 gm. dry weight of plant material.

chromatograms illustrated are of that fraction of the total extract that was adsorbed on activated alumina (acidic fraction), since at no stage of development was significant auxin activity found in the fraction that passed through the column.

The bulk of the auxin activity in stage I occurred in the indoleacetic acid position at an R_f of approximately 0·20 to 0·32. Frequently a faint pinkish spot developed in this position after treatment of the chromatograms with Salkowski's reagent, but it is by no means certain that this auxin is in fact indoleacetic acid. In one experiment in which this auxin was cut from the paper, eluted with 90 per cent. ethanol and re-chromatographed in the same solvent mixture, it was converted into another auxin having an R_f of 0·52 to 0·62, a behaviour which is not characteristic of indoleacetic acid. Auxin activity in this position was also found in stages II and III, but here there was a rather clear indication of a double peak (Fig. 2), suggesting the presence of two auxins which had not been completely separated in this solvent system. Chromatograms of Mission figs showed only a single peak in the IAA position.

Chromatograms of extracts of fruits collected on 21st June, when the auxin content was at its maximum, showed some activity in the indoleacetic acid position, but it is clear from Fig. 2 that the bulk of the auxin present at this stage of development is not indoleacetic acid, but some other auxin having a higher R_f value. This unknown auxin gave no Salkowski reaction and showed no fluorescence under ultra-violet illumination. It was active, not only in the *Coleus* test, but also in the coleoptile cylinder test where, however, its activity was somewhat masked through overlapping with growth-inhibitory substances on the chromatogram. Fig. 3 shows that this auxin was present in quantity, not only in the individual fruitlets, but also throughout the fleshy peduncle tissue of the syconium. In spite of the large quantities present it persisted only a very short time, having almost entirely disappeared by the next sampling on 1st July, after which there was no subsequent reappearance.

In addition to these main peaks of auxin activity, indications were obtained on some chromatograms of other substances showing biological activity in the *Coleus* test. These included both abscission-delaying substances (auxins) and abscission-promoting substances. Most chromatograms showed a small but significant auxin peak, of rather variable R_f value, running between the starting line and the indoleacetic acid position. Auxin activity in this position has been previously observed on chromatograms of many plant extracts, cf. the accelerator *a* of Bennet-Clark and Kefford (1) and *Malus* auxin 1 of Luckwill (17). Less consistent peaks of doubtful significance were several times observed at R_f values of 0·8 to 0·9. Definite indications of an abscission promoter at an R_f of 0·35 to 0·5 were observed in both varieties at all stages of growth except on 21st June, when such a substance, if present, would have been masked by the very large auxin peak in this position.

Endosperm development.

In previous papers attention has been drawn to the relationships which exist in the apple (13, 15) and the black currant (22) between auxin production in the seeds and endosperm development. For this reason particular attention was paid to the fig endosperm, the development of which has already been described in general terms by Condit (3). In the Calimyrna variety following fertilization the triple fusion nucleus undergoes rapid division to form a free nuclear endosperm and, at the same

time, the zygote divides slowly to form a small spherical embryo. Within a few days the endosperm becomes cellular and thereafter is digested by the embryo which, by this time, is in a stage of rapid growth and differentiation. The cells at the periphery of the endosperm, however, divide periclinally, forming a layer of small, regularly arranged cambium-like cells from which endosperm tissue is regenerated. Mature Calimyrna seeds (Fig. 4, A) contain a considerable bulk of this regenerated or secondary endosperm, which is utilized as a storage tissue for reserve protein and fat.

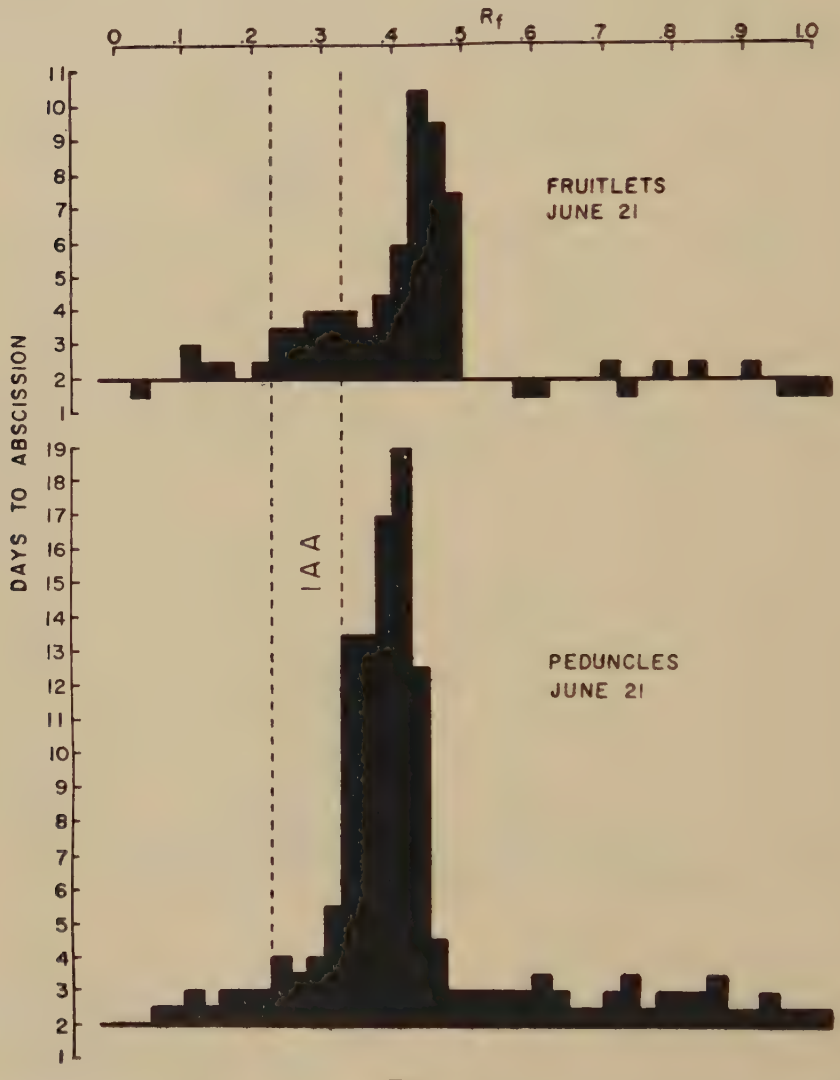

Fig. 3.

Chromatograms of ether extracts of fruitlet and peduncle tissue of Calimyrna fig fruits collected on 21st June. The chromatograms were loaded with an amount of extract equivalent to 1·5 gm. dry weight of tissue and were bioassayed in the *Coleus* petiole abscission test.

PLATE I.

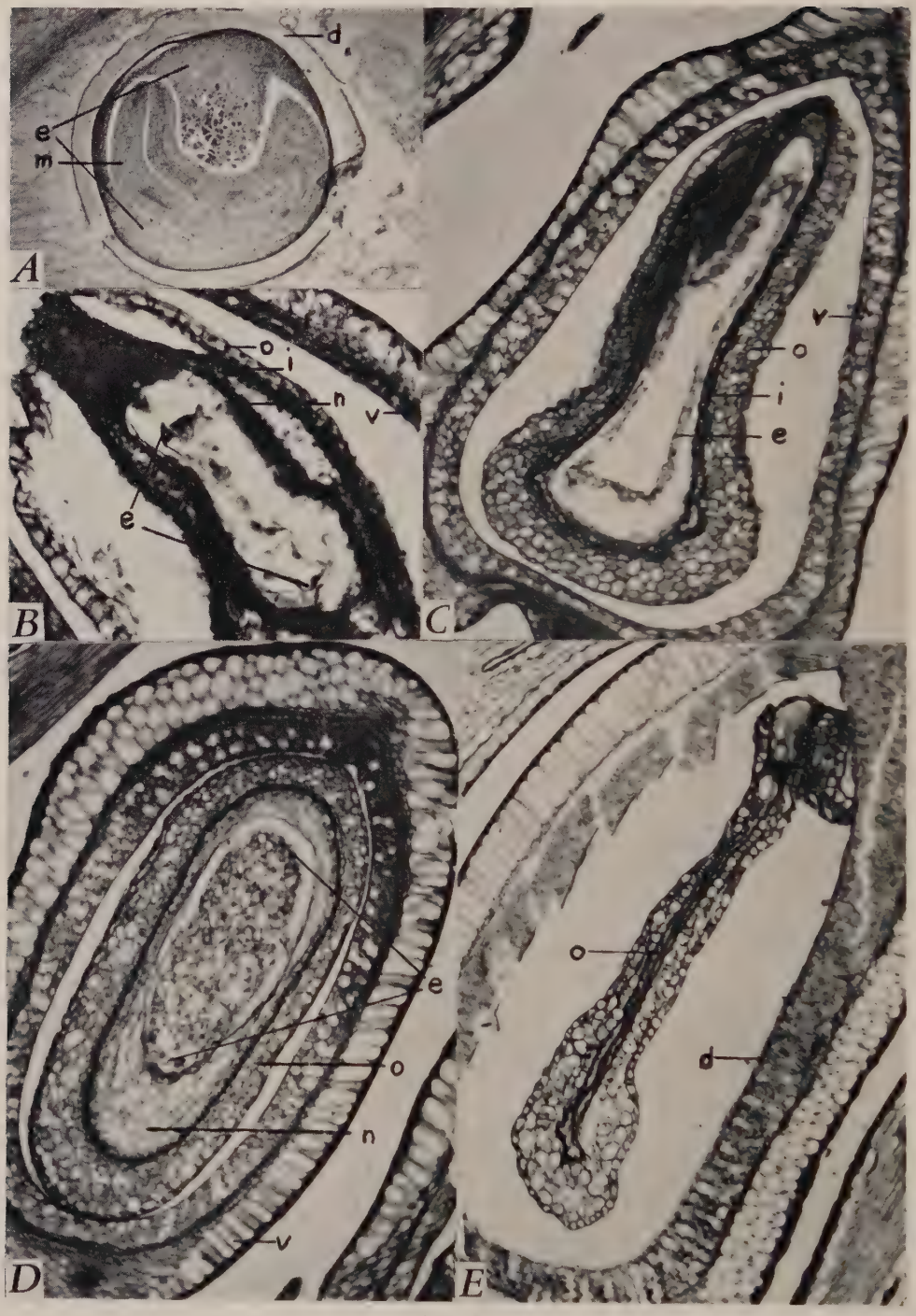

Fig. 4.

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The embryology of the Calimyrna fig is thus essentially similar to that described for the apple (13), except for the much shorter duration of the free nuclear stage and the somewhat more extensive development of secondary endosperm. The period over which endosperm and embryo development occur, in relation to the development of the fruit and to auxin content, is indicated in Fig. 1.

Normally, in the absence of fertilization, no growth of the endosperm and embryo occurs. The parthenocarpic varieties of fig, however, are exceptional in that they frequently develop a diploid parthenogenetic endosperm. This phenomenon is described by Longo (11, 12), Leclerc du Sablon (8, 9), Tischler (20) and by Condit (3) and seems to be general in the fig, having been reported in varieties belonging to each of the four major groups of the species. Because of its possible relationship to auxin production a special study was made to determine the duration and extent of development of parthenogenetic endosperm in Mission.

The first evidence of parthenogenetic endosperm appeared in fruits collected on 16th June. Development reached its peak a few days later and by 29th June the endosperm in some flowers was already showing signs of disintegration, such as pycnosis of the nuclei. By 6th July most of the ovules of Mission had collapsed as a result of the complete disappearance of both endosperm and nucellus. Such an ovule is shown in Fig. 4, E. However, in all fruits examined from the later collections a few ovules still contained some endosperm.

Much variability occurred in the extent of parthenogenetic endosperm development in the different ovules within a fruit, as was also found by Condit (3). In some the endosperm never advanced beyond the free nuclear stage of development, as shown in Fig. 4, B; in others a parietal layer of endosperm cells, consisting for the most part of a single layer, lined the enlarged embryo sac (Fig. 4, C). In a relatively few ovules the sac cavity was completely filled by a large mass of endosperm that more nearly resembled normal triploid endosperm (Fig. 4, D). From detailed studies made on fruits collected on 1st July it appeared that parthenogenetic endosperm was present in all the ovules, at least in the median region of the syconium.

Little evidence was found of parthenogenetic embryo development in this variety. As Condit (3) reported, the egg cell may or may not persist for a considerable

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Caption to Fig. 4.

Endosperm development in the fig.

A: section of mature seed of Calimyrna (×36) showing extensive endosperm around the embryo.

B: section of an ovule of Mission (×200) with a parthenogenetic endosperm in an early stage of development. A thin layer of cytoplasm and free nuclei lining the embryo sac has pulled away from the nucellus because of shrinkage during fixation. The intensely stained projections at the tip of the endosperm partially surround the egg cell. The egg and endosperm have been pulled away from the synergids, which remain attached to the nucellus.

C: section of a Mission fig ovary (×100) showing a thin layer of parthenogenetic endosperm which has become cellular and has developed to its ultimate extent. The nucellus has been almost completely absorbed and the ovule is beginning to collapse.

D: section of a Mission fig ovary (×100) with a mass of parthenogenetic endosperm filling the sac cavity.

E: section of a Mission fig ovary (×100) which has collapsed because of disintegration and absorption of endosperm and nucellus, leaving nothing but the integuments.

Key. e, endosperm; d, endocarp; m, embryo; o, outer integument; i, inner integument; n, nucellus; v, ovary wall.

period of time, but almost invariably the nuclei stained lightly and the nucleoli were small, both conditions indicating absence of incipient mitotic or endomitotic activity. Only one egg cell was found with a more intensely stained and enlarged nucleus, which probably had undergone endomitosis and, in a fruit collected on 28th July, one seed was found that contained an embryo—presumably parthenogenetic in origin. It appears, therefore, that parthenogenetic endosperm development is the rule rather than the exception in this variety, but that parthenogenetic embryo development, if it occurs at all, is very rare.

DISCUSSION.

The principal objective of this investigation was to determine whether there existed any relationship between the growth rate of the fig fruit and its auxin content at various times throughout the season. It is quite clear from Fig. 1 that no such relationship exists, at least as far as the concentration of total free auxin in the fruit as measured by the *Coleus* test is concerned. In Calimyrna the lowest auxin levels are found in the pre-pollination stage, when the growth rate of the syconium is at its highest. Furthermore, the sharp rise in auxin concentration following pollination is not reflected in any corresponding rise in growth rate, and throughout stage II, during which little increase in diameter occurs, considerable amounts of free auxin are found in the fruit.

The possibility remains that the growth rate of the fruit is limited, not by the total auxin complex, but by the concentration of one or more specific auxins, as is suggested by the work of Wright (22) on the black currant, the growth curve of which is rather similar to that of the fig. Chromatographic analysis of the fig auxins, however, does not suggest that this is so. It can be seen from Fig. 2 that there is no essential difference between the auxins of stages II and III, despite the wide difference in the growth rate of the fruit at these two stages of development. Neither is it possible in the fig to ascribe the restricted growth during stage II to the diversion of essential metabolites from the fruit flesh to the developing embryo and endosperm. Although this explanation might possibly apply to the seeded Calimyrna variety, it is obviously inapplicable to the parthenocarpic Mission in which endosperm development is of restricted duration and embryo growth is virtually absent. A further possibility, not investigated in these experiments, is that growth is controlled, not by auxins alone, but by the auxin/inhibitor balance.

In contrast to the lack of correlation with fruit growth there is a well-marked relationship between auxin production and endosperm development. This is especially convincing in the Mission variety, where the very large auxin concentration found in the fruits on 21st June coincides precisely with the time of optimum development of parthenogenetic endosperm tissue. A similar though smaller peak in the Calimyrna variety on the same date again coincides with the early stages of endosperm development in that variety. Reference to Fig. 2 shows that the auxin which appears in the fruit at the time of formation of the primary endosperm is of a different nature from those present at other stages of development. In R_f value it is similar to *Ribes* auxin 2, which Wright (22) found to be associated with endosperm development in the black currant, though the absence of a Salkowski reaction from the fig auxin makes it doubtful whether the two are identical. If this auxin does in fact originate in the endosperm it is remarkable how quickly it becomes diffused through-

out the whole tissue of the syconium, for already on 21st June it was found in high concentration throughout the peduncle tissue (Fig. 3).

The general auxin situation in the fig fruit is similar in many respects to that in the apple, described in an earlier paper by Luckwill (13). In both species there appears to be a close relationship between auxin production and endosperm development, but in neither is there any apparent correlation between auxin and fruit growth.

In the apple, the auxin which is associated with endosperm development appears to be the factor controlling the abscission of the young fruitlets and this may also be its function in the fig. In the Calimyrna variety, in the absence of pollination, no endosperm is formed and the immature syconia cease growth and drop from the trees unless they are sprayed with a synthetic auxin. In uncaprified Mission figs on the other hand, the auxin produced in the parthenogenetic endosperm is probably the factor which prevents abscission, thereby enabling the fruits to continue their development in the absence of pollination.

This study revealed no essential qualitative differences between the auxins of parthenocarpic and non-parthenocarpic figs, and the only marked quantitative difference was the somewhat higher auxin concentrations found in the non-parthenocarpic Calimyrna during the later stages of growth. This difference may be associated with the greater persistence of the endosperm in this variety as compared with Mission or with the growth of an embryo. It is of interest to note that Gustafson (7), in a comparison of the auxin content of seeded and parthenocarpic varieties of oranges, lemons and grapes, also found a higher concentration in seeded varieties during the later stages of fruit growth, though in the early stages the situation was reversed.

The general conclusion from this work is that, although auxin produced in the fig endosperm may play an essential role in preventing fruit abscission, the factor controlling fruit enlargement is probably not auxin-like in character. Moreover, the similarity in the growth curves of the parthenocarpic Mission variety, the seeds of which collapse at an early stage of development, and of the Calimyrna, which has normal seed formation, suggests that this fruit growth factor may have its origin in some tissue outside the seed.

SUMMARY.

(1) A study was made of the auxins in ether extracts of fruits of parthenocarpic Mission and non-parthenocarpic Calimyrna figs (*Ficus carica* L.) collected at weekly intervals throughout the season. The auxin extracts were chromatographed on paper in iso-propanol, 10; water, 1; ammonia, 1, and bioassayed in the *Coleus* petiole abscission test.

(2) No relationship was found between the concentration of " free " auxin in the fruit at different stages and its growth rate; neither was there a correlation with the concentration of any particular auxin. It was concluded that the factor controlling fruit enlargement is probably non-auxinic and may have its origin in some tissue outside the seed.

(3) In both varieties a sharp peak of auxin production occurred on 21st June (Fig. 1). In Calimyrna this corresponded with the time of formation of the primary endosperm and in Mission with the development of a parthenogenetic endosperm. The auxin which appeared in the fruits at this time had an R_f value of 0·35–0·50 (cf. IAA=0·20–0·32) and was different from those present at earlier and later stages

of development. The rôle of this auxin may be to prevent abscission of the developing fruits.

(4) The chief difference between the two varieties was the higher levels of auxin found in the non-parthenocarpic variety during the later stages of fruit development.

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EFFECT OF THE EARLY ENVIRONMENT ON THE DEVELOPMENT OF FLOWERING IN TOMATO

II. LIGHT AND TEMPERATURE INTERACTIONS

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In a previous paper (Calvert, 1957) it was reported that development of the tomato was modified by temperature during certain sensitive periods. The number of leaves formed between the cotyledons and the first inflorescence was reduced when the plants were grown at a low ambient temperature for a period of approximately nine days from cotyledon expansion.

Extending the period of low-temperature treatment beyond nine days did not cause further reduction in the number of leaves but did increase the number of flowers formed in the first inflorescence. Flower numbers in later inflorescences were also increased when low-temperature treatments were given at later periods.

The work of Reinders-Gouwentak (1954) shows that light conditions affect the number of leaves formed before the first inflorescence. When light periods of 9 and 12 hours of " high intensity " light from high-pressure mercury vapour lamps were lengthened by periods of " low intensity " light from incandescent lamps, both the number of leaves and the number of days to flowering were increased. Light intensities were not specified. de Zeeuw (1954) reports that the number of leaves formed before the initiation of the first inflorescence decreased when the light intensity was increased.

Differences in the number of leaves formed before the first inflorescence in plants raised in glasshouses at different times of the year have been reported by Goodall (1937) and Calvert (1955). Leaf number was greatest on plants raised near mid-winter when the daylength was shortest and the mean light intensity lowest.

Materials and methods.

In the experiments to be described, controlled or partially controlled environments for plant growth were provided by the following:

1. Growth rooms. Reference was made to these two rooms in the first paper in this series (Calvert, 1957).

2. Temperature-controlled cabinets. These cabinets, which were used inside glasshouses, were constructed from commercial Dutch lights and fitted with a small circulating fan and a 750-watt resistance net providing " black heat " controlled by a thermostat. Temperature was controlled satisfactorily at night and during sunless periods of the day. To compensate for the reduced light intensity within the cabinets, supplementary illumination was provided by three 80-watt " Daylight " fluorescent tubes mounted on top of the cabinets and controlled by a time switch.

3. Glasshouses. These had thermostatically-controlled heating systems which provided excellent temperature control at night and during sunless periods of the day.

Throughout the investigation, standard cultural techniques were adopted. Seeds were sown in the John Innes Seed Compost (JIS), 400-500 seeds per standard seed tray. As soon as the cotyledons had become horizontal (cotyledon expansion) the seedlings were pricked out into $3\frac{1}{2}$ in. pots containing John Innes Potting Compost No. 1 (JIP1).

Light intensities were measured with a selenium cell photometer calibrated against a sub-standard, tungsten-filament, projector lamp, previously calibrated by the National Physical Laboratory and operated at a filament temperature of 2854° K.

The data presented refer mainly to the mean number of leaves formed between the cotyledons and the first inflorescence and the mean number of flowers in the first inflorescence. These means will be referred to as "leaf number" and "flower number".

Results.

Duration and intensity of photosynthetic light.

In Experiment 1 two growth rooms were used in each of which there were four areas of different light intensity namely, 250, 500, 750 and 1,000 lumens/sq. ft. The ambient temperature was 60° F. (15·5° C.) during the light and dark periods in both rooms. The length of the light period was 8 hours in one room and 16 hours in the other. Seeds of varieties Potentate and Ailsa Craig were sown on 4th April 1956 and seedlings pricked out and placed in the growth rooms on 12th April. There were 20 plants per treatment.

Table I.

Effect of the intensity and duration of light on development of tomatoes (Exp. 1).

	Mean number of leaves				Mean number of flowers			
Variety	Potentate		Ailsa Craig		Potentate		Ailsa Craig	
Light period	8 hr.	16 hr.	8 hr.	16 hr.	8 hr.	16 hr.	8 hr.	16 hr.
250 lumens/sq. ft.	9·40	9·75	9·20	9·55	9·05	7·60	8·35	7·95
500 „ „ „	8·15	8·45	9·00	8·65	8·40	9·10	7·95	9·35
750 „ „ „	7·45	7·80	8·10	8·40	12·95	11·45	7·95	8·20
1,000 „ „ „	7·40	7·70	7·50	7·80	12·15	12·45	8·60	9·40
L.S.D. at 5% level	0·25		0·25		2·30		1·32	

After 4 weeks the plants were removed to a glasshouse where they were randomized on the benches. Later, the numbers of leaves and flowers were counted. The results, summarized in Table I, show clearly that there is a reduction in leaf number with each increase in light intensity, with both varieties and with both light periods.

In every comparison, except one, plants receiving 16 hours of light produced more leaves than those receiving 8 hours. The overall difference is significant at the 5 per cent. level. Nevertheless the differences are small compared with those at different light intensities.

With variety Potentate, flower number was significantly higher at intensities above 500 lumens/sq. ft. This was true at both the 8-hour and 16-hour light periods. With Ailsa Craig there were no significant differences in flower number at the 8-hour

light period but there was a significantly lower flower number at 250 lumens/sq. ft. when the light period was 16 hours.

Interaction of light intensity and temperature.

The two growth rooms were again used for Experiment 2. The same four light intensity areas were set up in each room but for this experiment the ambient temperature was 55° F. (13° C.) in one room and 65° F. (18·5° C.) in the other. The length of the light period was 12 hours in each room.

Seeds of Potentate and Ailsa Craig were sown on 28th April 1956 and the seedlings pricked out and placed in the growth rooms on 7th May. There were 20 plants per treatment. As in Experiment 1 the plants were removed to a glasshouse after 4 weeks and leaf and flower numbers were subsequently recorded. The

TABLE II.

Effect of light intensity and temperature on development of tomatoes (Exp. 2).

	Mean number of leaves				Mean number of flowers			
	Potentate		Ailsa Craig		Potentate		Ailsa Craig	
	55° F.	65° F.	55° F.	65° F.	55° F.	65° F.	55° F.	65° F.
250 lumens/sq. ft.	8·80	10·00	8·95	10·00	10·05	8·50	8·35	9·35
500 „ „ „	7·75	9·00	8·80	9·65	16·60	7·90	11·20	9·00
750 „ „ „	7·55	8·40	7·35	8·60	16·50	7·65	13·50	8·75
1,000 „ „ „	7·30	7·95	7·35	7·90	16·15	8·40	13·70	8·50
L.S.D. at 5% level	0·23		0·25		1·19		1·11	

results are summarized in Table II. The leaf numbers show that the two varieties responded very similarly to the treatments. Light intensity had the smallest effect on leaf number when the temperature was low (55° F.) and the smallest response to temperature occurred when the light intensity was high (1,000 lumens/sq. ft.). At 65° F. no significant differences in flower numbers occurred with either variety as a result of varying the light intensity, but at 55° F. significantly lower flower numbers were recorded when the light intensity was 250 lumens/sq. ft. and with Ailsa Craig there was also significance between flower numbers at 500 and 750 lumens/sq. ft.

Rate of leaf production and time of flower initiation.

In order to determine the duration of the vegetative period under different conditions of light and temperature, a further experiment (Exp. 3) was carried out in the growth rooms using the same four light intensities in each room as in Experiments 1 and 2. The temperature in one room was 59° F. (15° C.) and in the other 77° F. (25° C.). The daily light period was 12 hours in each room.

Seeds of variety Ailsa Craig were sown on 1st October 1957 and were pricked out and placed in the growth rooms on 11th October. From 16th October, dissections of the apices of 5 plants from each treatment were made every 2 to 3 days. From these were determined the rate of leaf production and the time of flower initiation for each treatment. Results are summarized in Fig. 1. The regression

equations are calculated from the means of the leaf initials present at each dissection. Plants from each treatment were deemed to have reached the flowering stage (F) when flower initiation had occurred in 3 of the 5 plant samples.

Because of the proximity of the regression lines in Fig. 1 the mean points have been omitted but the number of observations and the correlation coefficients are given. These results show that the rates of leaf production are linear and increase

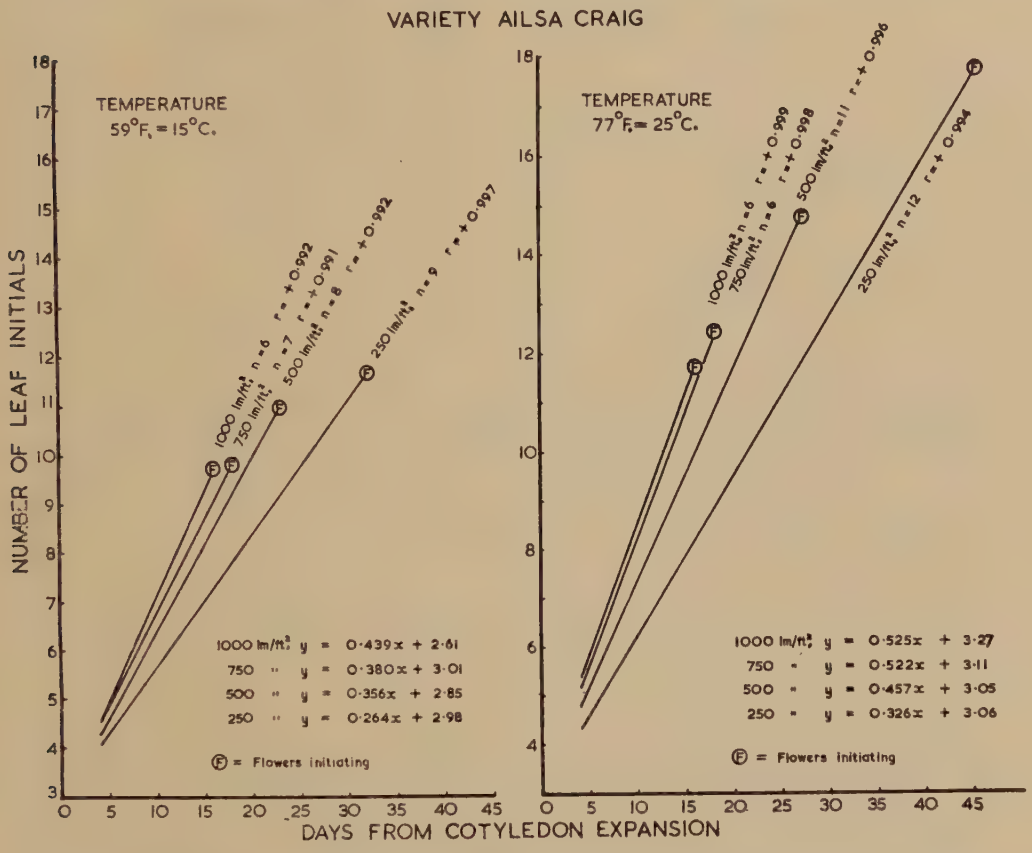
VARIETY AILSA CRAIG
TEMPERATURE
59°F. = 15°C.
TEMPERATURE
77°F. = 25°C.
NUMBER OF LEAF INITIALS
DAYS FROM COTYLEDON EXPANSION
1000 lm/ft.² n = 6 r = + 0·992
750 lm/ft.² n = 7 r = + 0·991
500 lm/ft.² n = 8 r = + 0·992
250 lm/ft.² n = 9 r = + 0·997
1000 lm/ft.² n = 6 r = + 0·999
750 lm/ft.² n = 6 r = + 0·998
500 lm/ft.² n = 11 r = + 0·996
250 lm/ft.² n = 12 r = + 0·994
1000 lm/ft.² y = 0·439x + 2·61
750 " y = 0·380x + 3·01
500 " y = 0·356x + 2·85
250 " y = 0·264x + 2·98
1000 lm/ft.² y = 0·525x + 3·27
750 " y = 0·522x + 3·11
500 " y = 0·457x + 3·05
250 " y = 0·326x + 3·06
F = Flowers initiating
F = Flowers initiating

FIG. 1.

Effect of light and temperature on rate of leaf production and time of flower initiation (Exp. 3). n, number of observations; r, correlation coefficient.

with both light intensity and temperature. They again show the effects of light intensity and temperature and the overall effect on the flowering time. Flowering occurred as early as 16 days after cotyledon expansion (1,000 lumens/ft.^{2} at 59° F.) and as late as 45 days (250 lumens/ft.^{2} at 77° F.).

Influence of cotyledon size.

Experiment 4 was made to test the effect of reducing the area of the cotyledons by cutting away half or whole cotyledons immediately after they had unfolded.

Seeds of Potentate and Ailsa Craig were sown on 15th August 1957 and pricked out on 24th August. On the following day portions of the cotyledons were removed. Details of the treatments are given in Table III. There were 12 plants per treatment.

TABLE III.

Effect of reduced cotyledon area (Exp. 4).

Treatment of cotyledons	Mean number of leaves to first inflorescence	
	Potentate	Ailsa Craig
Both entire	7·50	7·58
One halved	8·08	8·08
One removed	8·08	8·15
Two halved	8·42	8·25
One removed, one halved ..	8·92	8·75
Both removed	9·42	9·33
L.S.D. at 5% level	0·47	0·47

The plants were grown in an unheated frame for the first month and then placed in a glasshouse. The frame was carefully ventilated to avoid any undue rise of temperature. Leaf numbers were subsequently recorded and are summarized in Table III. It is clear that leaf number increases as the cotyledon area is reduced, the response of both varieties being almost identical. Goodall (1936) also recorded an increased leaf number following the removal of cotyledons.

Influence of sugar sprays.

At this stage of the investigation it seemed pertinent to enquire whether spraying the cotyledons with a sugar solution would increase their size and hasten flower initiation by reducing the number of leaves.

In Experiment 5, seeds of variety Potentate were sown on 6th November 1957 and pricked out on 14th November. They were then placed in three temperature-controlled cabinets set at 60° F. (15·5° C.), 65° F. (18·5° C.) and 70° F. (21° C.). In each cabinet there were three batches of ten seedlings, two of which were sprayed daily for the first 20 days with sucrose solutions at concentrations of 20 and 10 per cent. The controls were sprayed with water. A proprietary wetting agent was added to each solution and to the water. The length and breadth of the cotyledons were measured every two days and the product of these values taken as an index of cotyledon area. Area is plotted against time in Fig. 2. At the end of the treatment period the plants were randomized on a glasshouse bench and later the number of leaves and number of flowers recorded. This information is summarized in Table IV.

With regard to the effect of sugar sprays on cotyledon size, it will be seen from Fig. 2 that, at the end of the treatment period, cotyledons of plants sprayed with 10 per cent. sugar solution were not significantly different from the controls at 60° F. but were significantly larger at 65° F. and 70° F. Cotyledons of plants sprayed with 20 per cent. sugar solution were significantly smaller than the controls at 60° F. but not significantly different at 65° F. and 70° F.

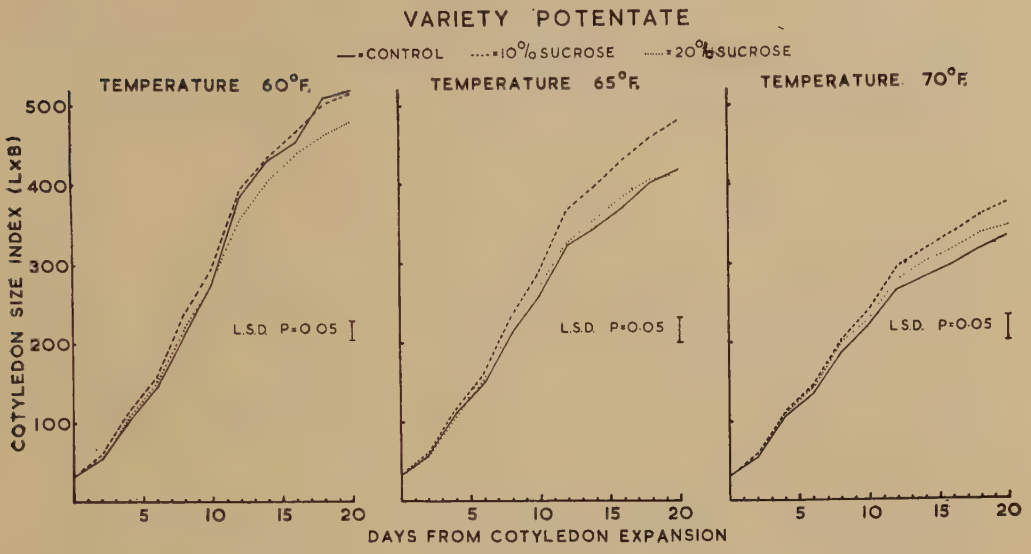

FIG. 2.

Effect of temperature and sugar sprays on rate of increase in area of cotyledons.

TABLE IV.

Effect of sugar sprays on development of tomatoes (Exp. 5); variety Potentate.

Treatments		Number of leaves to first inflorescence	Number of flowers in first inflorescence
Temperature	Sugar sprays		
60° F.	Nil	8·7	8·9
,,	10% sucrose	8·8	8·9
,,	20% ,,	8·9	7·4
65° F.	Nil	10·0	8·3
,,	10% sucrose	9·8	8·5
,,	20% ,,	10·3	8·5
70° F.	Nil	10·7	7·7
,,	10% sucrose	10·6	8·9
,,	20% ,,	10·9	7·5
L.S.D. at 5% level		0·67	1·98

The outstanding feature of these results is the marked effect of temperature on cotyledon size. At 60° F. the cotyledons were largest and the curves showing increase in area with time tended to be sigmoid. At 70° F. the cotyledons were smallest and the curves tended to be of the decrement type, i.e. the daily increase in area tended to fall from the start. Similar curves of increase in area of cotyledons of cucumbers have been published by Gregory (1928).

The mean numbers of leaves and flowers summarized in Table IV indicate no significant differences as arising from sugar sprays; temperature, however, again significantly altered leaf number, though not flower number. With the winter-light conditions prevailing at the time of the experiment it is unlikely that flower initiation occurred before the end of the treatment period.

DISCUSSION.

So far as the influence of photoperiod on flower initiation is concerned, the tomato is considered to be insensitive to day-length. Luckwill (1943) observed that *Lycopersicon esculentum* and *L. pimpinellifolium* flowered and fruited as well in a 12-hour as in an 18-hour day, though growth was somewhat retarded under short-day conditions. Further, tomatoes have for many years been grown in the artificial climates provided by glasshouses where growth could be maintained throughout the year but, in spite of large differences in day-length, so far as is known, plants have initiated flowers at all times of the year.

Reinders-Gouwentak (1954) has reported that the number of leaves formed in advance of the first inflorescence is affected by the " light conditions ", but since light intensities are not stated it is not clear from her experiments whether increase in leaf number resulted from an increase in day-length *per se* or from a period of low photosynthetic activity. It is obvious from Experiments 1, 2 and 3 of this investigation that a reduction in the intensity of the light promoting photosynthesis leads to an increase in leaf number. If leaf number is dependent on the total amount of light energy received by the plant, it might be expected that a reduction in the length of the light period would have the same effect as a reduction in light intensity, but in Experiment 1 this was not the case. Plants receiving 16 hours light produced significantly more leaves than those receiving 8 hours. It is possible that this significant though small difference could be attributed to a difference in the mean leaf temperature between plants in the two light periods. Although the ambient temperature as recorded on a bi-metallic thermograph remained constant during the light and dark periods, it is possible that the plants receiving 16 hours light had a higher mean leaf temperature than those receiving 8 hours, since they would receive radiant energy for a longer period in every 24 hours. It seems reasonable to conclude from this experiment that leaf number is markedly affected by differences in light intensity but not markedly so by differences in the total light energy per day when light intensities are the same. Goodall (1937) also concluded that increased leaf number was not due to a reduction in the total light falling on the plant but could be partly ascribed to low light intensity.

It will be seen from Fig. 1 that both leaf number and the rate of leaf production are affected by light intensity and temperature. Increasing the light intensity increased the rate of leaf production and decreased the leaf number, both effects contributing to a hastening of flower initiation. This was not true of the effects of temperature. The rate of leaf production increased with temperature but leaf number was also increased. Because of the opposite effects of light intensity and temperature the same leaf number may result from quite different combinations of light intensity and temperature, e.g., there were 11·7 leaves with 250 lumens/sq. ft. at 59° F. and also with 1,000 lumens/sq. ft. at 77° F. Similarly the same rate of leaf

production may result from different combinations of light intensity and temperature.

The interaction of light intensity and temperature on leaf number is clearly shown in Table II. With both varieties the range of leaf numbers was smaller at 55° F. but with variety Potentate the differences at 500, 750 and 1,000 lumens/sq. ft. were so small as to suggest that at this temperature further increases in light intensity might not further reduce the leaf number or, at a temperature below 55° F., leaf numbers might show little variation with the same four light intensities.

When the area of the cotyledons was reduced in Experiment 4 there was an increase in the leaf number. Thus, reducing the photosynthetic area of the plant had the same effect as reducing the light intensity.

The results of Experiment 5 showed that cotyledon size was reduced when the temperature was increased and this was accompanied by an increase in leaf number (Table IV). Cotyledon size was increased when 10 per cent. sugar solution was used at 65° F. and 70° F. but this increase was not accompanied by a reduction in the leaf number. Thus, although a reduction in the photosynthetic area of the cotyledons resulted in an increase in leaf number (Experiment 4), it was not possible to relate an increase in the size of whole cotyledons with a reduction in leaf number.

The effects of the light intensity and the light period on flower number are shown by the results of Experiments 1 and 2. They suggest that with both varieties fewer flowers will be produced when the light intensity is low and the temperature also is low, but at a high temperature flower number is not affected by the light intensity. There was no marked effect due to the light period.

The physiological aspects of these investigations will be discussed in greater detail elsewhere.

To turn to the practical aspects of the results, the time of initiation of the first inflorescence is an important factor in the production of early tomato crops. In Experiment 3 the combination of low light intensity and high temperature caused a considerable delay in the initiation of the first inflorescence and, though it is unlikely that such a high temperature would be maintained in practice, the results demonstrate the importance of reducing the temperature when the light intensity is low. On the other hand, when the light intensity is moderate or good, reducing the temperature may have less effect on the leaf number (Experiment 2) but may seriously retard the growth rate of the plants.

Since the publication by Lewis (1953) of data which showed that the number of flowers in the first inflorescence could be increased by reducing the temperature during a sensitive period, many commercial growers have attempted to introduce temperature reductions into their propagating techniques. It is clear from the results of Experiment 3 that the success of such methods will depend on the correct timing of the temperature reduction, i.e. on a correct assessment of the onset of flower initiation. Since the period between cotyledon expansion and flower initiation varies with the changing intensities of natural light, an accurate assessment of the duration of this period might be better made in terms of the light integral and the mean temperature. For earliest or most economical cropping it should eventually be possible to devise a light/temperature regime in which these components of the climate are adjusted on a daily basis.

Finally, the results of Experiment 4 are of practical interest since they show that an injury in the early stages of growth which results in a reduction in size of the cotyledons may delay flower initiation by increasing the number of leaves.

SUMMARY.

(1) The number of leaves produced before the first inflorescence ("leaf number") was influenced by the intensity of photosynthetic light, high light intensities causing low leaf numbers and vice versa.

(2) No major differences in leaf number occurred in plants grown in light periods of 8 hours and 16 hours at comparable intensities.

(3) By periodic dissections of the apex, the rate of leaf production and the mean date on which first signs of flower differentiation occurred were obtained for a range of environmental conditions. Signs of flowering were observed as early as 16 days from cotyledon expansion (1,000 lm./ft.^{2} at 59° F.) and as late as 45 days (250 lm./ft.^{2} at 77° F.).

The rate of leaf production increased with the light intensity but leaf number decreased. The rate of leaf production increased with temperature and leaf number also increased.

(4) The number of leaves formed in advance of the first inflorescence was increased when portions of the cotyledons were removed immediately after cotyledon expansion.

(5) Leaf and flower numbers were not affected by 10 per cent. and 20 per cent. sucrose solutions sprayed on to the cotyledons daily for 20 days from cotyledon expansion.

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EFFECTS OF ENVIRONMENT ON *RUBUS IDAEUS* L.

I. MORPHOLOGY AND DEVELOPMENT OF THE RASPBERRY PLANT

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THE red raspberry (*Rubus idaeus* L.) is an unusual species in that it bears woody short-lived shoots on a long-lived perennial root system. Each shoot passes through a well-defined sequence of seasonal phases during the course of its two-year life, which makes the plant an ideal subject for studying the effects of environmental factors on the processes of growth, flower initiation, and the induction and breaking of dormancy of vegetative and flowering apices. The present work has developed from earlier investigations on the factors which affect the regeneration of raspberry plants from roots (Hudson, 1954 and 1955), in the course of which it became necessary to raise a large number of raspberry plants in a series of growth rooms where temperature, day length and light intensity could be controlled within definable limits. The behaviour of plants in the various environments was so strikingly different that experiments were started to study these environmental effects, and the purpose of the present series of papers is (*a*) to describe the behaviour of raspberry plants in response to seasonal changes in a temperate climate, (*b*) to record experiments in which plants were subjected to controlled environments and to draw conclusions regarding the effects of various environmental factors on their behaviour, and (*c*) to show the extent to which the plant's reactions to certain environmental conditions can be modified by chemical treatments.

This introductory paper describes the main morphological features of the raspberry plant, defines a number of terms which will be used in referring to various parts of the plant, and specifies a series of distinct phases through some, or all, of which each raspberry shoot passes in its biennial cycle. The studies have been mainly concerned with the variety Malling Promise and, to a lesser extent, Lloyd George, but in most essentials these are believed to be typical of the varieties of red raspberry at present in cultivation in Britain.*

The natural habit of this species of raspberry is to form dense colonies of shoots, which originate from the roots or stems of the parent plant. Many young shoots are killed by cultivation or die from overcrowding, but those which survive subsequently develop long-lived, sparsely branched stools, and often become separated from the parent plant by the death of the parent roots from which they grew. The term

* The varieties of raspberries grown in Britain are all of the same " red raspberry " type, believed to have originated from the common wild species *Rubus idaeus*, L. On the other hand, three distinct types are grown in the United States, viz. red, black and purple raspberries. The first of these is probably, and the second and third are certainly, of different origin from the British varieties.

" colony " is used in these papers to refer specifically to the undisturbed development of a single plant.

Raspberry shoots arise in three distinct ways—as root suckers from buds on roots, as stem suckers from axillary buds (usually basal buds borne near ground level) or, more rarely, as lateral branches from axillary buds well above ground level. It is necessary to make these distinctions since each type of shoot behaves in a different way in response to environment. The most convenient way of describing the raspberry plant is to follow the development of one shoot, from the time of its origin as a root bud to the death of most of the shoot after fruiting (Fig. 1A). The morphology of the perennial part of the plant (the stool) will be described in a later paper.

Phases of growth of a raspberry shoot.

The morphology of a shoot depends on (*a*) whether the apical meristem is producing leaf or flower primordia, (*b*) whether those primordia expand or not and, if the former, on what the rate of expansion is, and (*c*) on whether the internodes elongate or remain short. The successive phases of development in the raspberry shoot illustrate various combinations of these types of behaviour (Hudson, 1958).

Phase 1: Initiation of the root bud.

Under natural conditions root buds arise laterally from uninjured raspberry roots. They are abundant on the roots of most important varieties, though not on all, and can be found at all times of the year, although they are capable of elongating only during an " on " season, which extends from about August to April (Hudson, 1954).

Phase 2: Subterranean sucker.

When a root bud commences to grow, a small number of its proximal internodes elongate rapidly, carrying the growing point (which is protected by scale leaves) towards the surface of the soil (Fig. 1B). Subterranean suckers can grow considerable distances to the surface and examples more than 50 cm. long have been found in the course of root excavations.

Phase 3: Emergent sucker.

Under many environmental conditions, which will be described in detail in later papers, elongation ceases shortly after the tip of the shoot emerges above soil level, but leaves commence to expand at once in a characteristic pattern that results in the formation of a tight rosette of leaves. Although neighbouring buds on any piece of root usually vary considerably in size, buds of all sizes are capable of elongating under suitable conditions. The habit of the rosette and the form of the first leaves depend to some extent on the size of the root bud when it commenced to elongate. Rosettes which form at, or just above, soil level will be referred to as " primary rosettes " to distinguish them from rather similar rosettes that form at the distal ends of long shoots, far above ground level (see Phase 6).

Thus in the first three phases the three major phenomena of vegetative apices, namely leaf initiation, internode elongation and leaf expansion are separately dominant in turn.

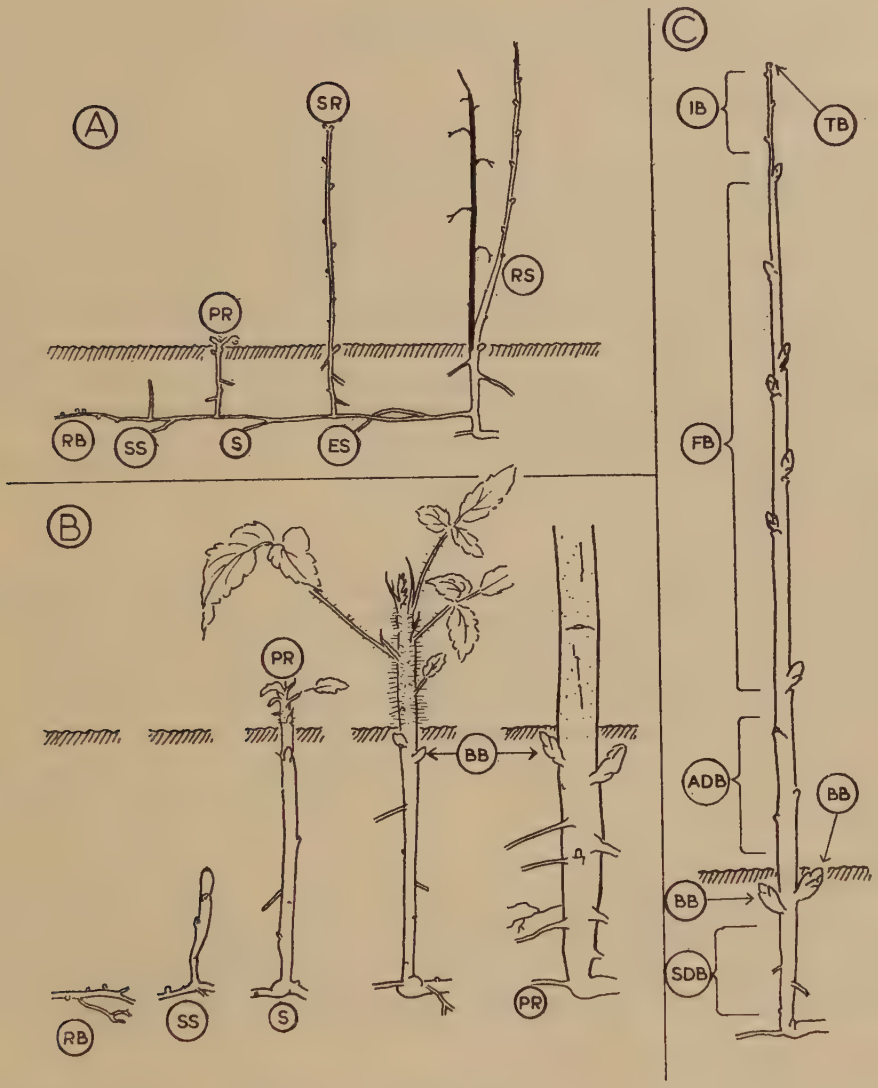

FIG. 1.

Diagrams showing the parts of young raspberry plants.

A. Shoots in various stages of development on a two-year old plant in autumn.
B. Growth of root suckers, showing the early prominence of basal buds which provide for the next generation of fruiting shoots.
C. Classification of buds on a mature shoot, foreshortened for the purposes of the diagram.

Key. RB, root buds; SS, subterranean suckers, elongating but not yet emergent; S, emergent sucker, with a primary rosette (PR) of leaves just above ground level; ES, elongated shoot, which has a terminal secondary rosette (SR); RS, replacement shoot; TB, terminal bud; IB, immature buds; FB, fruit buds; ADB, aerial dormant buds; BB, basal buds, from which replacement shoots will grow; SDB, subterranean dormant buds: PR, parent root connecting sucker to parent plant.

Phase 4: First winter dormancy.

Where shoots emerge in late summer or autumn, most of the leaves of the rosette are shed during the winter, when the terminal apex is dormant.

Phase 5: Elongating shoot.

After a pause (in Phases 3 and 4), the duration of which depends on environmental conditions, the next stage is the rapid elongation of the shoot (new cane), which is lignified and characterized by the development of a clothing of prickles.* This phase commences in spring in temperate climates and continues until the autumn, during which time elongating shoots often grow up to six or eight feet long in Britain. This is not the limit of vegetative growth, since much longer shoots may be produced in climates more favourable to this phase of growth, as in some parts of New Zealand, or under controlled environmental conditions. At about the time that the shoot starts to elongate, adventitious roots are produced freely from the subterranean portion of the stem or " sucker base ", i.e. that part which lies between the point of origin of the root bud and the soil surface.

By contrast with Phases 1, 2 and 3, leaf initiation, internode elongation and leaf expansion proceed concurrently throughout this phase.

Phase 6: Initiation of flower buds.

The shoot ceases to elongate at the end of the growing season and produces a small, but distinguishable, secondary rosette of leaves at its tip. At the same time most of the axillary meristems initiate flower primordia and can then be referred to as dormant fruit buds since they are, at that time, still incapable of growing out. Leaves become senescent and fall. Up to the stage of flower initiation various terms have been used to refer to the mature vegetative shoot, viz. the " turion " of Rydberg, quoted by Bailey (1932); the " primocane " of Bailey (1932); the " young cane " of Brierley (1930); and the " sterile cane " or " first year cane " of traditional North American usage.

Anomalous Phase 6: Tip flowering.

In some varieties of raspberry (e.g. Lloyd George) the apical meristem sometimes initiates flower primordia in early autumn while elongation is in progress, so that a late crop of flowers and fruit develops on a terminal inflorescence before the shoot becomes dormant—the " second growth " referred to by Wood (1949).

Phase 7: Breaking dormancy of flower buds.

Except in Anomalous Phase 6, raspberry flower buds have a cold requirement for breaking of dormancy and cannot begin to grow until this has been received. By spring time the cold requirement has normally been met in Britain and buds are ready to grow with the onset of warmer weather but it is interesting to note that in slightly warmer climates (e.g. in the more northerly parts of New Zealand), or in mild

* " Cane ", the traditional horticultural term for the aerial raspberry shoot, can also refer to rooted suckers, growing away from the parent plant and used as planting material—e.g. the " cane nursery " of Grubb and Harris (1945), Wood (1949) and others. It is usual practice in horticulture to refer to the shoot as a " new cane " from the time when it starts to elongate in spring until it starts to fruit in the following year, when it becomes the " old cane ".

winters in Britain (Harris, 1940), there may be insufficient winter cold to break dormancy, in which event the flower buds fail to grow, or grow abnormally and fail to flower.

By spring time a variety of conditions can be recognized in the axillary buds on a mature shoot, which can be classified as follows, working downwards from the apex of a shoot (Fig. 1C):

Terminal bud: this develops into an inflorescence if it survives, but it is often killed by winter conditions, except, of course, where tip flowering and death of the apex occur in the autumn.

Immature buds: comprising a few buds below the apex, which are potentially fruit buds but often fail to develop and die in winter.

Fruit buds: comprising most of the aerial buds, which have by then initiated flower primordia. It is these buds that produce the crop of fruit.

Aerial dormant buds: a few buds towards ground level which normally fail to elongate, although they may be capable of doing so if stimulated, producing the " sterile (vegetative) laterals " of Bailey (1932), or the " parcifrond " of Bailey (1941).

Basal buds: one or more of the buds, originating in the axils of leaves or leaf scales at or just below ground level, which commence to swell at a very early stage in the development of the vegetative shoot. By the following year these buds are more prominent than any others on the cane, and it is from them that the next generation of canes is produced.

Subterranean dormant buds: a succession of buds, borne on the stem base below ground level, which normally remain dormant and ultimately die. They can, however, produce stem suckers if stimulated into growth, especially by damage to the basal buds and upper part of the cane.

Phase 8: Flowering and fruiting.

When the dormancy of the fruit buds has been broken by sufficient winter cold, they commence to grow with the onset of suitable weather conditions, producing mixed fruiting laterals which bear both leaves and flowers (the " novirame " of Bailey, 1941). At the same time one (or more) of the basal buds starts to elongate vigorously into a vegetative replacement shoot, which repeats the biennial cycle described above. The term " fruiting shoot " will be used for the normal raspberry shoot which is fruiting in its second season (the " old cane " and " second year cane " of common usage and the " floricane " of Bailey (1932)).

Anomalous Phase 8: Flowering on new shoots.

Occasionally a replacement shoot initiates flowers and produces fruits from all its axillary buds in the autumn of the season in which it grew from a basal bud. This is referred to as a " basal flowering shoot " (the " paucirame " of Engard (1945), although he was referring to another *Rubus* species), to distinguish the behaviour from tip flowering. This behaviour is infrequently observed in the varieties Lloyd George and Malling Promise in Britain, and more frequently in the former variety in New Zealand. Such shoots die after fruiting, hence they can be regarded as annual rather than biennial. The habit is common or normal in a number of other *Rubus* species, e.g. in *R. rosaefolius* Smith referred to by Engard.

Phase 9: Senescence and death.

After fruiting, the whole shoot dies back to the position from which a replacement shoot has grown. The bases of successive shoots form the perennial structure, referred to as a " stool ", which will be described later.

DISCUSSION.

The biennial life cycle of the raspberry shoot thus consists of a succession of apparently distinct phases. At the outset it was postulated that these could be explained as the responses of the shoot to seasonal changes in a temperate climate, and later papers will show to what extent this basic hypothesis has been confirmed by experiment. In considering the relation between the raspberry plant and its environment it was argued that, if the passage from phase to successive phase is largely, or even entirely, in response to environment, then plants should always behave in the same way in any particular environmental conditions and it should be possible to hasten or delay the sequence at will or to arrest development at any phase. Thus, subjecting plants to suitable environmental treatments might lead, on the one hand, to the production of fruits on very young plants, or alternatively, to the maintenance of plants in one of the phases for prolonged periods of time. If, on the other hand, the progress from phase to phase is due in the main to endogenous reactions within the plant itself, this fact would be manifest when plants of different past history were grown together in a similar environment, since they would be likely to behave differently. A third possibility is that progress through the various stages might depend partly on internal factors such as, for example, the physiological age of the shoot, and partly on the influence of environment. Such a system of " dual control " would be demonstrated if plants failed to pass from one phase to the next, even when in a suitable environment, until after the lapse of a certain minimum time, or until they had made a minimum amount of growth; or if they ultimately passed on to the next phase without any change in the environment. The experiments described in some of the later papers in this series were designed to investigate the relative importance of internal and external factors in determining the behaviour of the raspberry plant, particularly with regard to the passage of the shoot through the series of phases referred to above.

SUMMARY.

The main morphological features of the raspberry plant are described, and a number of terms used for reference to the various parts are defined.

Shoots arising as suckers from root buds pass through nine distinct phases, in each of which the pattern of growth and development is different. This series of papers is concerned with the effects of environmental and endogenous factors on these phases of growth.

ACKNOWLEDGMENTS.

It is a pleasure to acknowledge the contributions which my colleagues I. H. Williams and J. A. Mackenzie have made to these studies. The extent of their personal contributions will become apparent from the authorship of subsequent papers. I should also like to acknowledge the technical assistance which has been

given by various members of the Department including Miss E. M. Marshall, D. H. G. Smith and R. Wilson.

Much of the work described in subsequent papers has been made possible by financial grants from the Agricultural Research Council.

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EFFECTS OF ENVIRONMENT ON *RUBUS IDAEUS* L.

II. FIELD OBSERVATIONS ON THE VARIETY MALLING PROMISE

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Department of Horticulture, University of Nottingham School of Agriculture, Sutton Bonington

YOUNG raspberry plants, variety Malling Promise, each consisting of a rooted vegetative cutting with only one shoot, were planted in May 1955, six feet apart each way in the open ground. Cultivation was reduced to a minimum to enable the habit of the plants to be observed under the natural conditions of a temperate climate.

From August onwards root suckers began to emerge around the parent plants, at first from adventitious buds on the main roots, which grew out more or less radially and horizontally, although this pattern was later partially obscured by the growth of suckers from lateral roots. In this manner a large number of new vegetative shoots developed around, and at some distance from, each parent plant. In earlier studies Hudson showed that the emergence of root suckers in the field follows a consistent seasonal pattern. During the period between August and April, suckers appear above soil level whenever climatic conditions permit of their elongation, and this has been termed the " on " season, since a high percentage of root cuttings taken at any time during this period will regenerate successfully. During the period between May and early August few, if any, new root suckers appear above ground and root cuttings taken during this " off " period generally fail to regenerate.

For the present work it is convenient to divide the " on " period into three parts. Newly emerged suckers could be found at any time from August to early November and again from March to early May but, during the intervening period, i.e. from about the middle of November to the latter part of February, no new suckers appeared in the field. Root buds are viable during this period, since root cuttings taken at any time during the winter regenerate readily even at moderate temperatures in growth rooms or glasshouses, and failure of suckers to appear in winter out-of-doors is probably due to the restriction of their development by low soil temperatures. The numbers of root suckers recorded in fortnightly periods in 1955-56 are shown in Fig. 1 but earlier and later observations suggest, as would be expected, that slight variations occur from year to year in the dates when these three periods begin and end.

Behaviour of emergent suckers in autumn.

Root suckers which emerged from August to November elongated little above soil level. After making a maximum of only a few centimetres of growth, and often less, the rate of elongation declined, although leaves continued to expand, and the

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shoots developed the primary rosettes of leaves around the apical growing points which are characteristic of autumn suckers. The height of the suckers, and the extent of rosette development, appeared to be governed largely by the time of emergence in relation to climatic conditions. Those which emerged earliest produced well-developed rosettes but later suckers, appearing in October or early November,

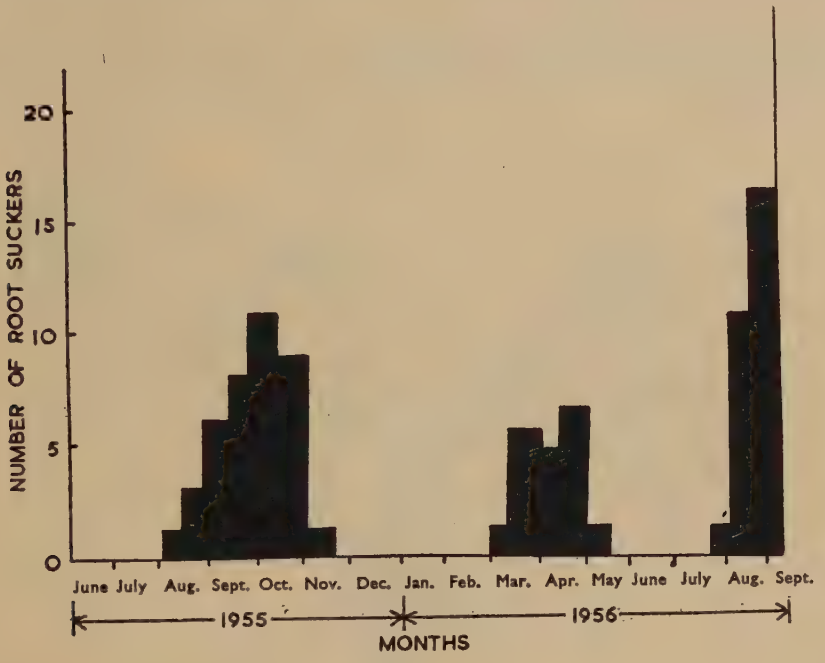

FIG. 1.

Number of new root suckers that emerged above ground during fortnightly periods from July 1955 to September 1956 (average of 12 parent plants) in the first sixteen months after planting.

produced little more than a resting bud close to soil level. Fig. 2 shows the stages of development reached before the onset of winter dormancy by shoots emerging at successively later dates.

Root suckers examined in November exhibited the following characteristics. Leaves showed a graded range of types from scale leaves below ground, through simple (juvenile) leaves to compound types with three or five leaflets. Buds in the axils of leaves formed between soil level and the rosette were smaller than those in the axils of scale leaves immediately below soil level. The latter buds are of considerable interest since they represent the specialized basal buds from which replacement shoots develop at a later stage in the biennial cycle. The portion of stem which bears these specialized buds is referred to as the " replacement zone ". Although, in the field, these buds do not normally develop into shoots until the parent root sucker has produced fruiting laterals in its second year, they can already be distinguished by their larger size more than a year earlier.

During the ensuing winter, most of the leaves of the rosette are shed. The leaf

bases persist and probably serve to protect the apical meristematic region. In the following spring the apical meristem resumes visible activity, new leaves expand and the root sucker enters a period of rapid vegetative growth to become an elongating shoot.

Behaviour of suckers emerging in spring.

A new succession of root suckers began to appear above soil level in March 1956 and continued until early May, this being the second (spring) period of natural emergence which is a characteristic of the " on " season in the field. Although the

FIG. 2.

Types of rosettes which form on root suckers emerging in autumn at successively later dates. All drawn in early November. *a*, appeared above soil level in August 1956; *b*, appeared above soil level in September 1956; *c*, appeared above soil level in late September 1956.

first few internodes above soil level appeared to be shorter than those immediately below, these suckers did not pass through any distinct resting period at emergence, nor did they produce noticeable rosettes of leaves. Instead, they showed a continuous transition from the scale leaves of the underground portion to the fully expanded leaves above soil level, and from the elongated internodes below soil level to those of the elongating cane above.

In such cases the replacement zone was far less well-defined and axillary buds, both in the leaf axils above soil level and in the axils of scale leaves below the ground, were considerably smaller than were those of suckers which emerged in the autumn.

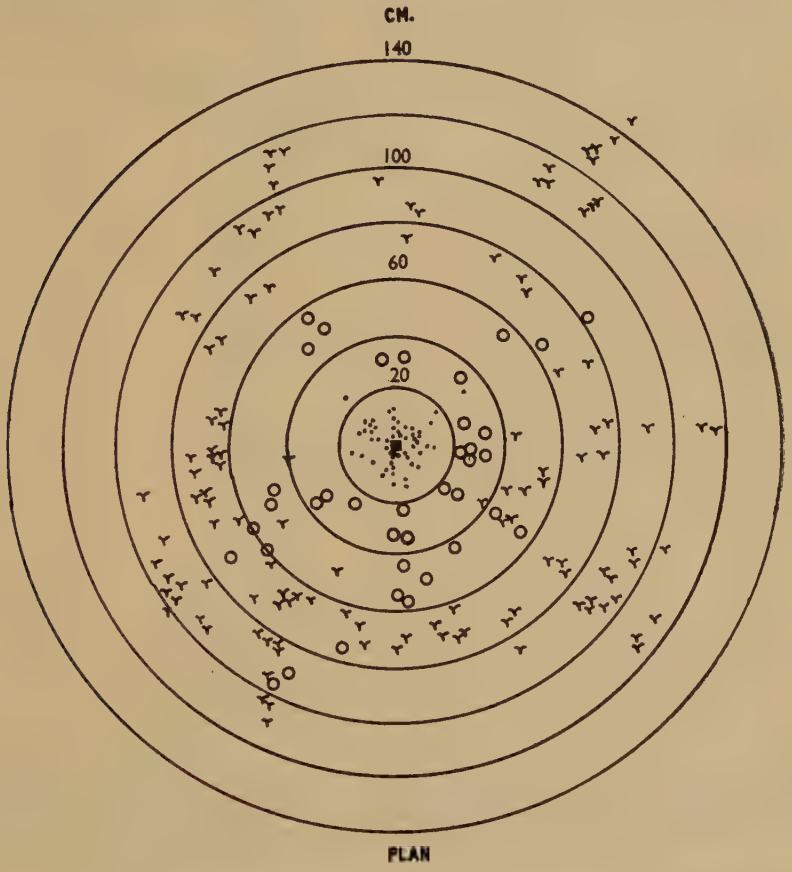

FIG. 3.

Distribution of successive batches of suckers emerging around a typical plant which had been set out as a single rooted shoot in May 1955; suckers plotted as they emerged until December 1956. ·, suckers emerging August–November 1955; o, suckers emerging March–May 1956; Y, suckers emerging August–November 1956.

Distribution and elongation of emergent suckers.

Fig. 3 shows the distribution of root suckers developing from a single parent plant during the first eighteen months after planting. Suckers which emerged in the

first period of the " on " season lay largely within a radius of 20 cm. from the parent shoot, whereas those which appeared in the spring period of the " on " season occurred mainly between 20 and 80 cm. from the parent. All the suckers elongated in the spring and early summer of 1956, and no more emerged until the autumn, when a large number of new suckers appeared as far as 140 cm. from the parent and mainly distal to the previous flush. Thus successive " waves " of suckers, appearing during each period of emergence, arose largely distal to the earlier ones, showing the effective manner in which this plant can spread and colonize the ground. This habit is less

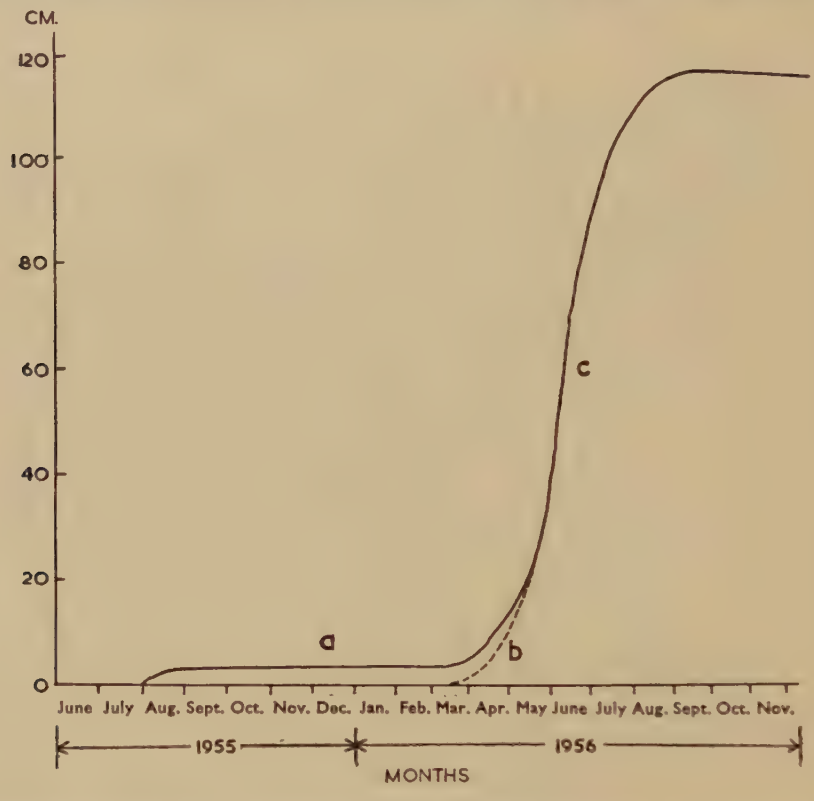

FIG. 4.

Elongation of raspberry shoots in 1955 and 1956 (average of 18 shoots), showing the behaviour of suckers which emerged in autumn 1955 (*a*) and in spring 1956 (*b*). Behaviour of both groups was similar once strong elongation had begun (*c*).

apparent with plants in ordinary cultivation, where the annual crop of new root suckers between the rows is normally removed.

Once elongation began in the spring the behaviour of root suckers was similar, whether they had emerged in the previous autumn and experienced a dormant phase, or in the spring without any appreciable check to growth. Shoots elongated rapidly and at an increasing rate until late May or early June, after which the rate declined. Elongation ceased entirely in late August or early September (Fig. 4), by which time some shoots had reached a length of nearly two metres. Marked apical dominance

was shown during this phase of vegetative growth and little branching occurred unless the tip of a shoot was damaged or broken off. Cessation of growth in length coincided with the onset of flower initiation in axillary buds, a phenomenon which will be discussed in subsequent papers.

DISCUSSION.

The growth phases and morphological differences which occur in the emergent root sucker suggest a close relationship between changing environmental factors and the habit of development. Before passing to the next part of the investigation, in which the effects of controlled environments will be considered, the general behaviour of raspberry root suckers growing under field conditions can be summarized as follows, in relation to the gross seasonal changes which occur in the environment:

August-November	Shortening days and falling temperatures	Autumn period of sucker emergence; cessation of elongation of vegetative shoots.
September-November	Shortening days and falling temperatures	Terminal rosettes of leaves are formed; basal buds in the replacement zone increase in size.
November-February	Shortest days and lowest temperatures	No further apparent development of suckers which have already emerged, or emergence of new ones; leaves fall from terminal rosettes.
March-early May	Lengthening days and rising temperatures	Renewed activity of the apical meristems of emerged suckers; new leaves open and shoot begins to elongate on the original axis of growth; emergence of new suckers, which elongate without rosetting and with no clearly-defined differentiation of basal buds in the replacement zone.
Mid-May-July	Longest days and highest temperatures	Period of maximum shoot elongation; no new root suckers emerge.

SUMMARY.

A study of the growth and development in the field of root suckers of the raspberry variety Malling Promise is described. Differences in the behaviour of root suckers appearing in autumn and in spring are considered in relation to changes in climatic factors. The present paper ends at the stage when the mature vegetative shoot ceases elongation.

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ECOLOGY OF THE BLACK CURRANT GALL MITE (*PHYTOPTUS RIBIS* NAL.)

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NOTHING has been published on the biology of the black currant gall mite in Britain since Massee (1928) gave an account of the life history. He indicated that galled buds contained thousands of mites but gave no actual counts. Some further observations were made in a paper on chemical control by Jary, Austen and Pitcher (1938). The present paper summarizes work on some aspects of population and infestation levels and of behaviour in relation to bush development.

Experimental procedure.

A series of counts over a two-year cycle has been made on the variety Wellington XXX at Sutton Bonington. The method of estimating the population was to take two groups of five obviously galled buds from mature bushes at approximately fortnightly intervals. The buds were gently broken up, placed in 100 c.c. water plus 0·5 c.c. wetting agent, soaked for one hour and then stirred mechanically for 20 minutes. Counts were made by examination of the mite suspension on a 1 c.c. counting slide under a binocular microscope and the total mean population per single gall calculated. The means of 15 such duplicated counts were estimated to have a standard error of 7·5 per cent.

RESULTS.

Annual population cycle.

Fig. 1 shows that there are two extended egg laying periods whose peaks are separated by a regular interval of six months. Eggs were not found in new buds invaded in the spring until some time in late June. Their numbers then increased to a peak in late September and declined to a very low level for about a month to six weeks in mid-winter. At this time the mean population of the galled bud averaged between 3,500 and 4,500. In January, egg laying began again and the population in the gall built up to a maximum of about 25,000 to 35,000 by late March. After this there was rapidly increasing loss through movement of the mites out of the galled buds. The galled buds taken for counting were of average to large size. Individual small galls were found to contain correspondingly small numbers of mites with maxima about a quarter of those quoted above, while the very largest galls would have nearly double the number.

The development of eggs in two distinct periods separated by a winter break of several weeks and the long time between first invasion of the new buds in April and the first appearance of eggs in June would suggest that individual mites are long-lived and the whole population cycle could be accounted for by only two generations

of mites ovipositing over a long period. A further suggestion that this might be so is provided by the occasional discovery of apparently non-breeding mites in very small numbers in buds of normal appearance during the winter. Savzdarg (1957), however, working in the U.S.S.R. has suggested a total of five whole generations divided between the two main breeding periods.

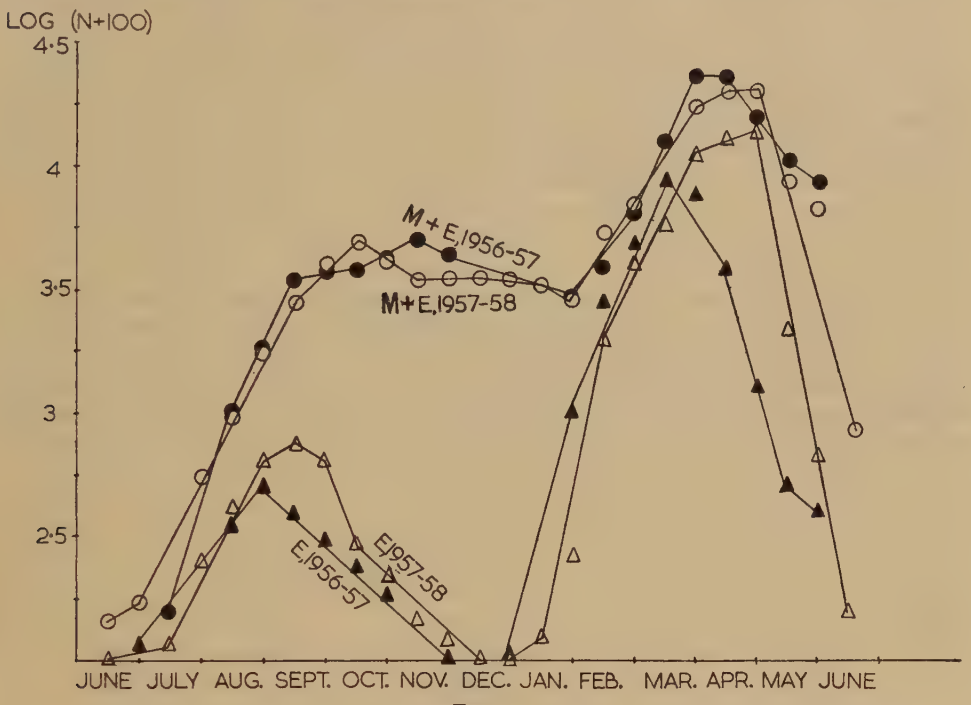

FIG. 1.

Fortnightly population counts per gall shown as log(N+100) transformed estimates. ●, 1956-57 total mites plus eggs; O, 1957-58 total mites plus eggs; ▲, 1956-57 total eggs; △, 1957-58 total eggs.

Migration of mites.

When leaving the old gall in spring, the mites wander freely over the stems and into the fresh growth, also frequently tumbling off the gall in small groups. This movement occurs throughout the blossom period from the late " grape stage " onwards and coincides with rapid shoot growth and new bud formation. This can be expedited by bringing shoots into a warm room at any period after midwinter. However, this does not appear to be a simple temperature effect acting directly on the mite itself, since mass migration cannot be induced on shoots treated similarly in late autumn, although occasional single individuals were found on the surface of the buds during a warm sunny spell in October 1957.

Mass movement out of the old gall occurred over a much shorter period in the spring of 1958 than in that of 1957. In 1958 about 97 per cent. of the mites left the old galls during a migration period of seven weeks compared with less than 60 per cent. in 1957. New buds were found invaded on 24th April 1958, which was about the same date as in 1957, a season of earlier growth. Small numbers of mites had

penetrated into the centres of new buds where they remained for several weeks without causing apparent damage to the tissues of the bud. Oviposition inside the bud began at the same time as flower rudiments were forming in uninfested buds.

Not all mites leave the old galls but, in the East Midlands over the three seasons 1956 to 1958, more than 90 per cent. of the galls had withered by mid-June. Some remained until much later with a small residual population of mites but these did not appear to have any practical importance in relation to the development of a fresh infestation. Lees (1917) noted that the penultimate buds on growing shoots were seldom galled in the West Country and considered that these were formed too late to become infested. This effect has not been noted in the East Midlands where almost all new buds have become visible by fruit set. An examination of large numbers of shoots from several plantations did not reveal any particular pattern of gall development. In general, the middle buds of a new shoot tended to be most frequently galled but the position of fresh galls did not seem to be directly related to that of the nearest old gall.

A very small proportion of the mites developing from old galls actually achieve successful colonization of new buds. It is calculated that with a bush of about 2,000 buds—a normal average for a medium-sized mature bush—any existing level of galling would be carried into the next season by a final survival in the new buds representing less than 1 per cent. of the total mite population developed from the old galls on that bush. Fig. 2 shows the relationship between the percentage infestation

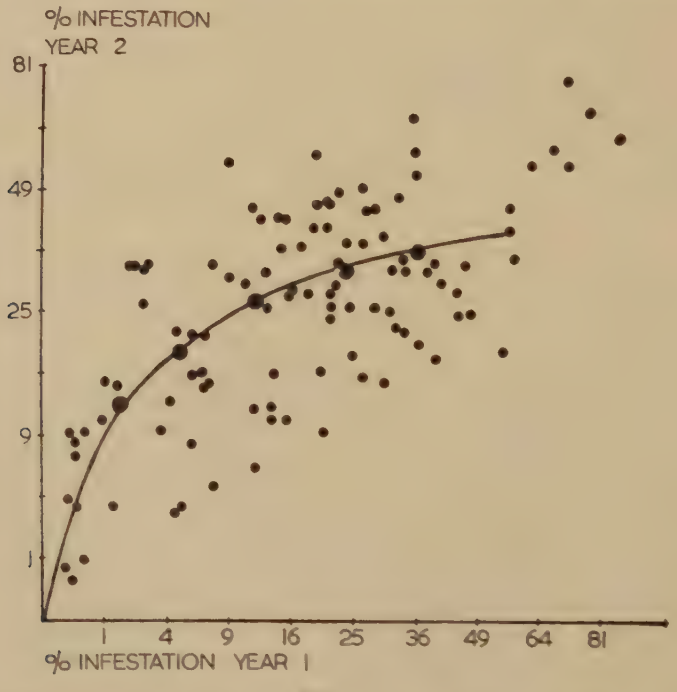

FIG. 2.

Relationship of per cent. bud infestation in two successive seasons on the same plots. Points plotted on square-root scale. Curve drawn through means of grouped data.

of any one year with that on the same plot in the previous year. It is seen that the regression is not linear. With low initial counts up to about 15 per cent., there is generally a rapid build-up in the succeeding year. With counts approaching about 35 per cent. in the first year of observation, build-up tends to cease so that an apparent balance is maintained at about this level and higher counts in the first year may actually decline in the second year. In the graph, a square-root transformation has been used owing to the rather wide dispersion of individual points and so as to enable the lower category counts to be shown. The curve has been drawn through the means of grouped data. From the graph it may be seen that infestations of 1, 9 and 25 per cent. in the first year become on the average 9, 25 and 32 per cent. respectively in the second year. In practice, the increase in commercial plantations is seldom so rapid, since the use of miticides, even when relatively inefficient, tends to delay the rapidity of build-up.

Period of most active migration.

Experiments on the contamination of supposed mite-free, rooted pot plants were carried out so as to test the practical implications of the long migration period. In 1957, series of pots were placed in an infested plantation at fortnightly intervals from early April to mid-June. It was found that plants in each series showed galling the following autumn, regardless of the date at which they had been exposed to contamination and of whether they had been placed immediately against infested bushes or at a distance of 4 ft. from their centres. In 1958 the experiment was repeated in a different form. Potted seedlings were contaminated by placing heavily galled shoots in each pot for periods of a week. There were 9 pots in each series with weekly periods extending from 16th April to 4th June. Results expressed as percentage galled buds and mean mite population per bud were recorded in November. The series of 4th June was left exposed to contamination throughout that month and it will be seen from Fig. 3 that these plants developed a somewhat higher

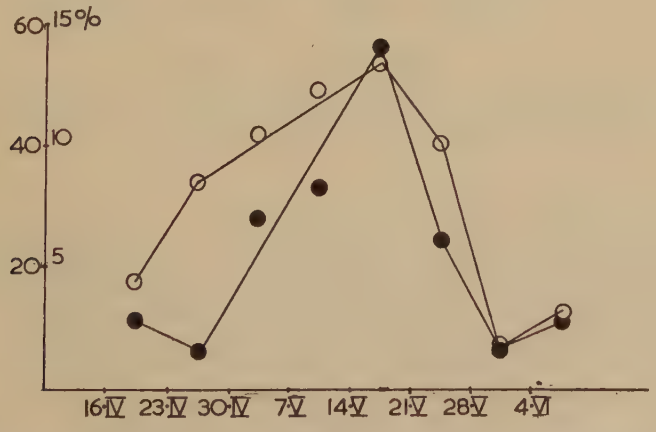

FIG. 3.

Infestation transference experiment, 1958. Base line, period of contamination, 16th April to 4th June. Counts in November, 1958: ●, mean mite population per bud (scale on left of ordinate; O, per cent. infested buds (scale on right of ordinate).

infestation than the series exposed to contamination in the previous week. The series exposed to infestation in mid-May developed the largest numbers of galls and mites. Although some infestation developed on plants of each series from mid-April onwards it was evident that the most critical period from the point of view of devising a satisfactory spray programme was in mid-May or about the period immediately following full blossom.

Practical confirmation of the importance of this period was obtained from trials where series of plots were sprayed with endrin at different dates from grape stage to fruit swell. Fig. 4 shows that, in both 1957 and 1958, best control was obtained with single sprays applied at fruit set while those applied at grape stage were least satisfactory. The latter has been the traditional period for spraying black currants,

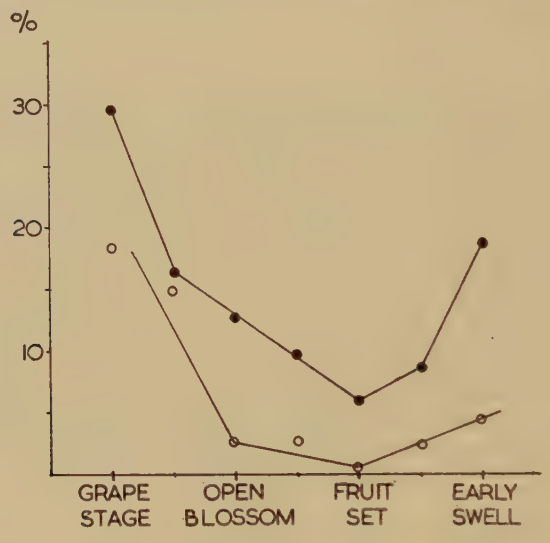

FIG. 4.

Spray timing experiment with endrin. Base line, stage of flower/fruit development at time of spray application. ●, mean per cent. infestation in November, 1957 series; O mean per cent. infestation in November, 1958 series.

adopted largely in order to avoid the spray damage that later applications of lime sulphur might occasion. However, it should also be noted that endrin and sulphur differ in their activity in that endrin will destroy mites that have already invaded a new bud while it is still in the early stages of development, so that the optimum period of use for these two miticides may not necessarily coincide.

Fig. 5 gives a generalized diagram of the life cycle of mite and host plant.

The economic damage resulting from mite infestation of the bush has not been fully investigated. The presence of mites in a new bud, even in very low numbers down to about six, seems to have the effect of completely suppressing flower formation, while a bud that is infested to the extent that visible galling will later develop does not normally produce extension growth in the spring. However, one or more

secondary buds occasionally develop within the outer scales of the gall and these may give rise to grossly distorted foliage and more or less abnormal flowers. A general reduction in vigour occurs when infestation reaches a level of 30 per cent. or more and leader growth is replaced by the production of many short twiggy side shoots.

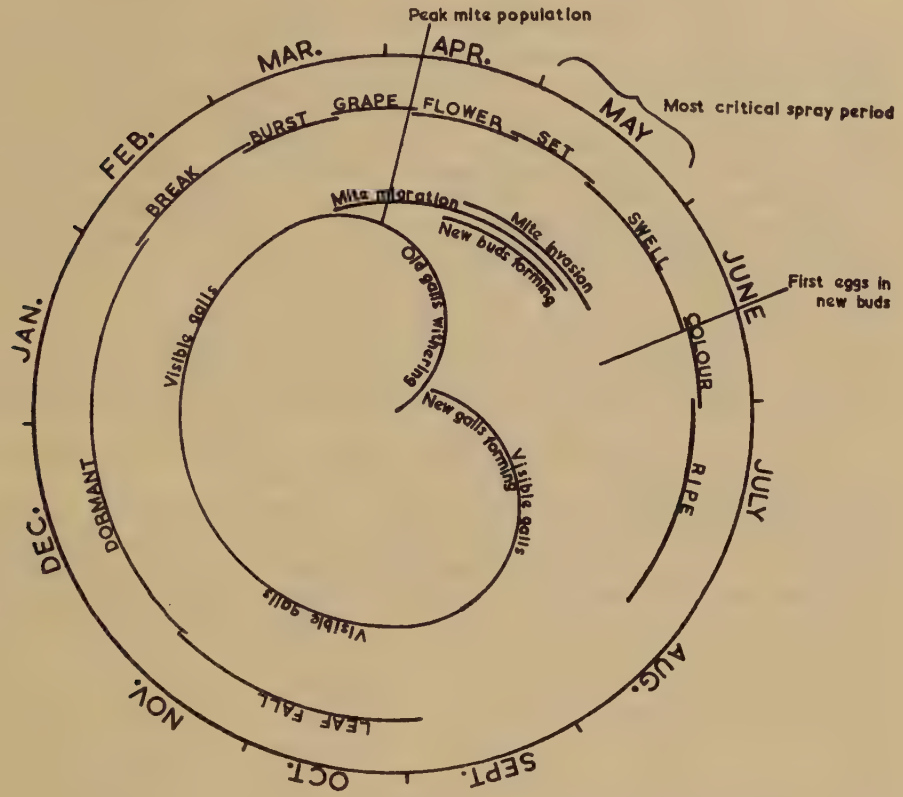

FIG. 5.
Diagram illustrating cycle of bush growth and mite behaviour.

ACKNOWLEDGMENTS.

The facilities afforded by the Management Committee of the University of Nottingham, School of Agriculture, Sutton Bonington, are gratefully acknowledged. Thanks are also due to Mr. H. Ferne of H. Burtt and Sons, Dowsby and to Messrs. H. W. Carters Ltd. for the provision of clean rooted cuttings and seedlings.

SUMMARY.

Fortnightly estimates of numbers of mites and eggs showed that average peak populations of 4,000 and 30,000 individuals per galled bud were reached in October and late March respectively. Eggs first appeared in the new gall in late June,

several weeks after mite invasion began in April. They reached a maximum in late September and declined to a minimum by late November. Oviposition began again in January and there was a heavy population build-up until late March after which numbers began to dwindle through migration of mites from the gall. Migration was most intense throughout and just after the blossom period.

Plot samples taken in successive seasons showed that infestations built up rapidly until gall development reached a level of about 35 per cent. after which an apparent equilibrium was reached. Contamination of mite-free plants with infested material showed that infestations could be transferred at any period from early grape stage to fruit swell, but peak invasion, as measured by population estimates and gall counts in the autumn, occurred in the period immediately following full bloom. Both in 1957 and 1958 single applications of endrin gave best control at fruit set.

The direct effects of mite injury include suppression of flower development in invaded buds, localized foliage distortion and the proliferation of side shoots at the expense of extension growth.

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AN INSTRUMENT FOR MEASURING THE FIRMNESS OF BRUSSELS SPROUTS

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One of the most important criteria of quality in Brussels sprouts is firmness, yet there have been few recorded attempts to measure this objectively. In Danish and Dutch variety trials respectively (Hansen *et al.*, 1950; Jensma and Kraai, 1954) sprout firmness has been assessed subjectively, presumably by hand pressure. In Britain, Finch (1952) records the sorting of sprouts from variety trials into two grades, the first grade comprising those which are " really firm and well-shaped ", and, since few sprouts are misshapen, this grading system is essentially a subjective measurement of sprout firmness. A similar grading has been used at the Scottish Horticultural Research Institute (North and Frith, 1957), and we have also attempted to assess firmness objectively by estimates of the relative density, from the formula:

$$D = \frac{\text{Wt. of 50 sprouts in oz.}}{(\text{Mean diameter of sprouts in inches})^3}$$

It was appreciated that D is not an accurate measurement of relative density because sprout shape varies between varieties, and the cube of the mean diameter does not therefore truly represent the relative volumes of all sprouts. Nevertheless, D seems to give an objective measurement of firmness because those sprouts which feel especially firm or soft to the touch have respectively high and low values for D. Moreover varietal values of D were found to be significantly correlated with the corresponding proportions by weight of 1st grade sprouts of the total varietal yields. However, it was thought that none of the techniques for measuring firmness was sufficiently accurate to detect small differences and that some type of pressure tester was necessary for this purpose.

Pressure testers for various horticultural products have been in use in the United States for about 30 years and a review of the most important types is given by Haller (1941). Most of these instruments were designed for testing apples, pears, peaches and plums, and they measured the force required to thrust a blunt needle a given distance into the fruit. Instruments working on this principle largely measure shearing strength and do not give a satisfactory assessment of sprout firmness, which is essentially a measurement of elasticity. However, Verner (1931) has designed a different type of pressure tester for stone fruits which determines the force required to squeeze the fruit a given distance between two flat surfaces. More recently Hamson (1952) has described an instrument, based on similar principles, for measuring the firmness of tomatoes in terms of the distance through which the fruit is compressed by a weighted plunger. The instruments described by Verner and by Hamson give objective measurements of firmness in a way which simulates the squeezing of the fruit between thumb and forefinger and it was thought that this principle could be applied to the measurement of firmness of Brussels sprouts.

Materials and methods.

During November 1957, several experimental pressure testers were constructed at the Scottish Horticultural Research Institute. The aim was to devise an instrument based on a similar principle to that of Hamson but of a design which would make it possible to measure the uncompressed sprout, apply the weight system and remeasure the compressed sprout in a single operation. The main practical difficulties in the designing of the instrument were: (1) to prevent excessive friction on the moving parts of a weight system sufficiently heavy to give a reasonable degree of sprout compression, and (2) to provide steady and gradual application of the weight system so that its impact on the sprout did not cause undue compression.

A prototype which gave reasonably good results was tested during the spring of 1958. The faults of this instrument were discussed with Mr. J. C. Forrest, Ministry of Agriculture, Fisheries and Food Research Establishment at Aberdeen, who suggested several modifications. An improved instrument was constructed incorporating the use of guide blocks for the weight system, the lifting of the weight system vertically by means of a cable instead of by direct action of a lever to the weight frame, and the hydraulic damping of the weight frame.

The improved instrument is illustrated photographically in Fig. 1 and diagrammatically to scale in Fig. 2. It is built on a framework of 20 gauge sheet iron with three channel-sectioned horizontal cross members of 17 gauge (M1, M2, M3 in Fig. 2).

The mechanism consists of a light plastic rod (R) 1 cm. in diameter suspended from a chain (C) which passes over two sprockets (S1 and S2) and is nearly counterbalanced by a weight (W). One of the sprockets (S1) actuates a pointer (P) which records, on a graduated dial (D), the distance in millimetres between the lowest end of the rod (R) and the top of a sprout holder (H) which is a brass cylinder having a slightly concave upper surface. The chain is Meccano sprocket chain and the sprockets are Meccano parts No. 96a; this combination moves the pointer through 360° for 6 cm. vertical movement of the plastic rod. Surrounding the rod, but without making direct contact with it, is a 2 kg. weight system (L); this is supported on two guide rods passing through guide blocks (B) bolted to each of the cross members (M2 and M3) and the rate of its downward movement is controlled by a hydraulic damper (A) (filled with grade 90 motor oil), which is pivoted to the central horizontal cross member (M2). Resting against, but only lightly touching, the guide rods is a stabilizer (E) fitted to the top of the plastic rod; this prevents the rotation of the rod and the consequent twisting of the chain (C). The weight system is lifted by a wire passing over a pulley (U) operated by the handle (O), and in this direction the damping system offers negligible resistance to movement. After moving a short distance it engages with, and lifts, the plastic rod through contact with a metal stop on it (T1). When the handle (O) is released, the downward movement of the rod is immediately checked by any object on the sprout holder, but the weight system does not bear on the rod until the hydraulic damper (A) allows it to sink to the metal stop (T2).

To operate the instrument, the handle (O) is rotated and the plastic rod thus raised; a sprout is placed on the sprout holder (H) and the handle (O) is released. The rod comes to rest on the top of the sprout, the diameter of which is recorded on the dial (D). After about five seconds the weight system thrusts on the rod and the diameter of the compressed sprout may be read when the pointer has ceased to move

PLATE I.

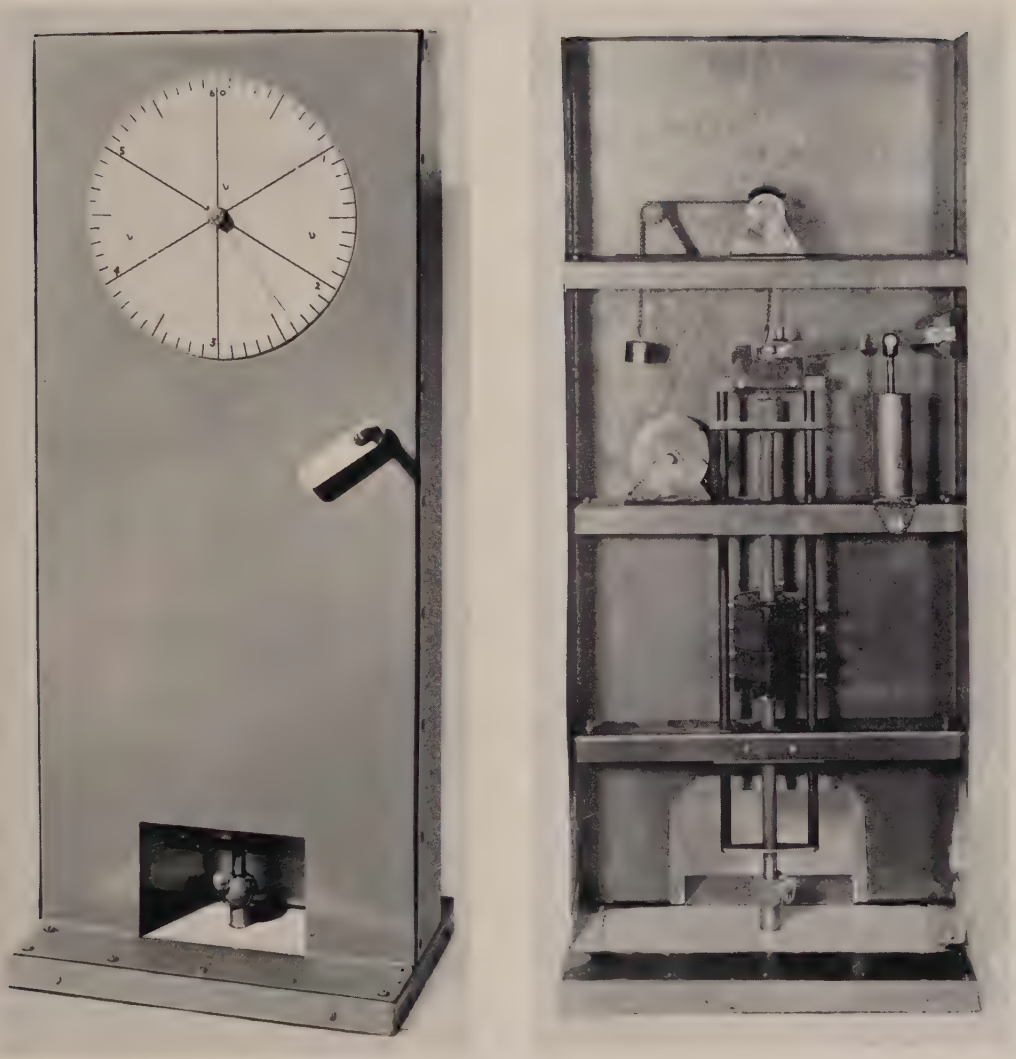

Fig. 1.
Instrument for measuring firmness of Brussels sprouts.
Front and rear views.

[face page 184

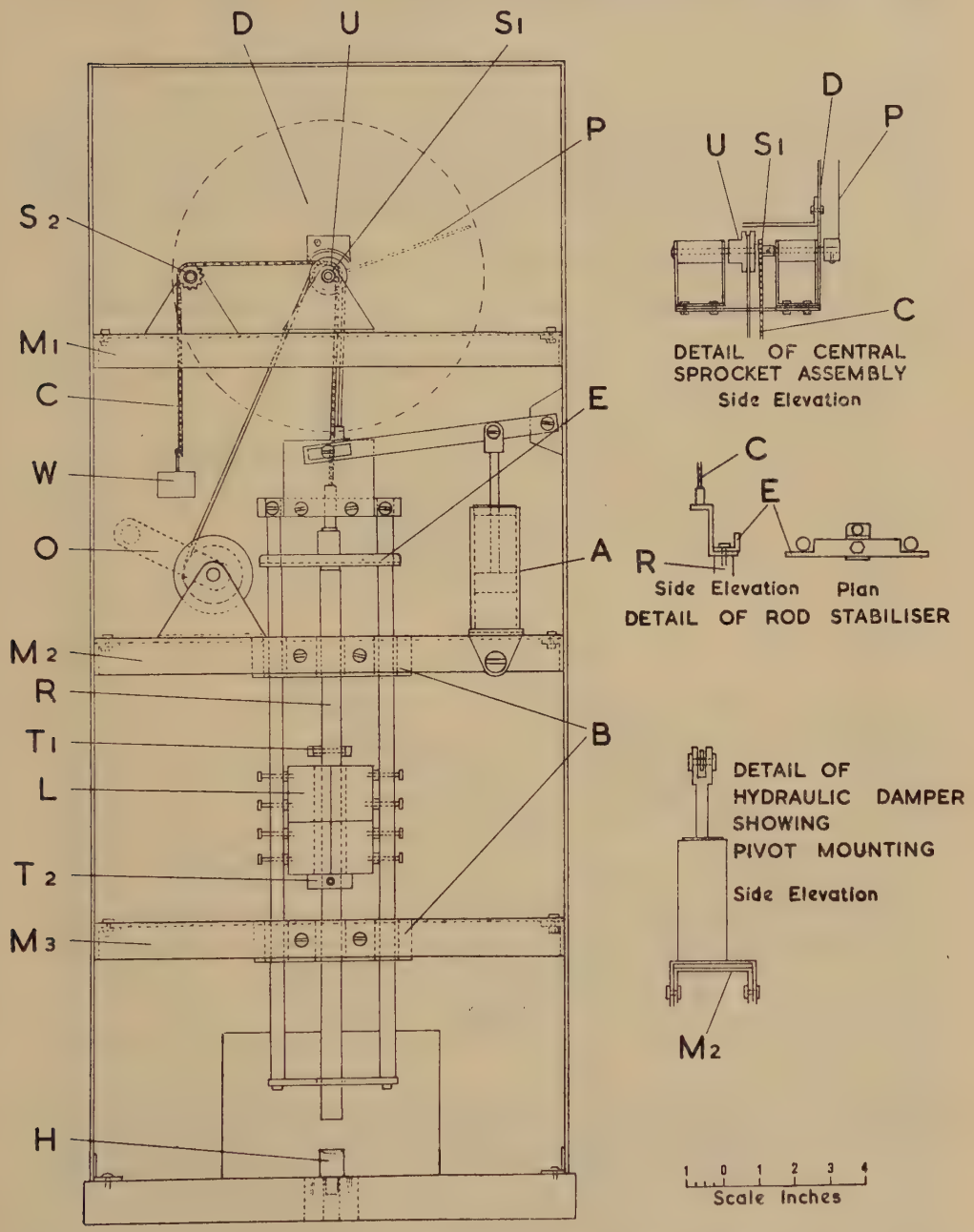

FIG. 2.

Diagrammatic rear elevation of sprout pressure tester.

perceptibly, viz. in 6-10 seconds. The relationship of the diameter of the sprout before and after compression is taken as a measurement of firmness.

Results.

To find how the amount of compression of a sprout is related to its size, the relationship between the degree of compression of a given material and its thickness was studied. Tests were made with the instrument on four substances: solid rubber, foam rubber, gelatine and plastic foam. The results given in Fig. 3 show, especially

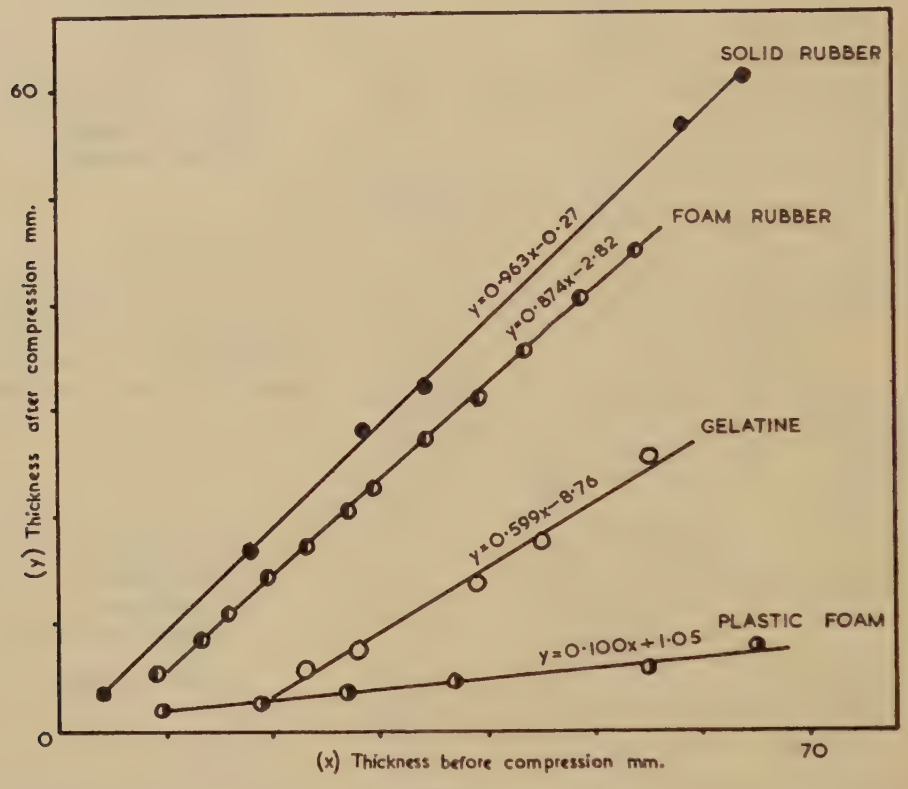

Fig. 3.

Relationships between thickness of four materials before and after compression in pressure tester.

from the curve for gelatine, that the thickness after compression is not invariably an exact linear function of the thickness before compression. Nevertheless, between the limits of the readings taken, the relationship can be expressed reasonably accurately as a linear function. However, none of the calculated linear regression lines passes through the zero point of the graph so that the ratio of thickness before compression to that after compression is not constant for all thicknesses of material and does not therefore give a consistent assessment of firmness. Only for solid rubber, in which case the second constant (−0·27) of the regression is small, does

this ratio give a measure of firmness that is nearly independent of the thickness of the material.

To ascertain if firmness of Brussels sprouts might be reasonably accurately expressed, as with solid rubber, by the ratio of thickness before and after compression, linear regressions were calculated for 120 sprouts from each of four strains. The second constants were quite small (—0·27, —0·11, —0·26, —0·59), showing that the diameter of a compressed sprout, expressed as a percentage of its diameter before compression, should give a consistent representation of its firmness.

The procedure which has been adopted for measuring firmness of sprouts from a field trial is as follows. The harvest from a plot is spread out on a table and the unmarketable stalks, loose leaves and very loose unsaleable sprouts are discarded. A random sample of 20 sprouts is then taken and the lateral diameter of each sprout is measured before and after compression in the instrument. The sprouts are always measured with the axis horizontal; arranging them with the axis vertical gives firmness figures which are higher and show smaller varietal differences though a similar varietal ranking for firmness. In five variety trials at Invergowrie, each with six replications and 11–13 varieties, ranges of 6–11 per cent. difference in firmness have been recorded between the varieties with the firmest and those with the softest sprouts in the trial. With standard errors of 1·2–1·5 per cent., significant differences in varietal sprout firmness have been demonstrated. As examples of well-known varieties: in one trial the firmness for the variety Cambridge No. 1 was 77·3 per cent. and for Cambridge Special 85·0 per cent.

DISCUSSION.

The instrument described here gives measurements of sprout firmness which do not depend on personal judgment and which, on this account, are superior to the subjective assessments of firmness which rely on hand pressure. It also gives more reliable estimations than those obtained by the objective method for determining firmness by means of the relative density, as no satisfactory technique for rapidly assessing sprout volume has yet been recorded.

In practice the instrument will clearly show varietal differences in sprout firmness. It takes about ten minutes to measure the firmness of 20 sprouts by the procedure described. This is as quick as any other recorded method except the simple assessment of firmness of individual sprouts by hand. However, if an assessment of sprout size is required in addition to firmness, the instrument will give results as quickly as simple hand assessment, for it measures size simultaneously with firmness.

The instrument should provide a basis, not only for comparing varieties and lines of breeding material, but also for more fundamental studies on the inheritance of sprout firmness and the effects of climate and cultural treatment. It requires no periodic calibration so that results from different centres and different years may be validly compared.

SUMMARY.

A pressure tester for assessing the firmness of Brussels sprouts is described. It measures the diameter of a sprout before and after compression by a plunger 1 cm. in

diameter to which a 2 kg. weight is applied. The diameter of the sprout after compression, expressed as a percentage of that before compression, is a measurement of sprout firmness. The instrument shows significant differences in firmness between varieties and it is suggested that it is sufficiently accurate for use in studies of inheritance and the effects of climate and cultural treatment on sprout firmness.

ACKNOWLEDGMENTS.

We wish to acknowledge the valuable contributions made by Mr. J. C. Forrest, head of the Engineering Section at the Ministry of Agriculture, Fisheries and Food Research Establishment at Aberdeen, towards the improvement in the design of the prototype instrument. Our thanks are also due to the staff of the factory workshop at Aberdeen for constructing the instrument described in this paper. Without this co-operation it would not have been possible for us to make use of the improved instrument in 1958.

We are also indebted to our colleague Dr. A. R. Wilson for his helpful suggestions and the interest he took in this project.

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(*Received* 30/1/59.)

BOOK REVIEWS

THE FUNDAMENTALS OF GARDENING. Edited by W. E. Shewell Cooper. The Ullswater Library. (London: Seeley, Service & Co. Ltd. 1958. Pp. 304, illus. Price 25s.)

This book is attractive in appearance and of great interest to read. True to its title, it is concerned with the most fundamental subjects of the garden, and the many chapters are written by eminent authorities in a delightfully free and informal manner, quite unlike the ordinary text-book.

The first four chapters, written by Sir Bernard Keen and Sir John Russell, are an important contribution and give a most excellent description of the soil from its origin to a state of fertility.

The next chapter deals in a somewhat superficial manner with drainage and is mainly concerned with methods of watering, from water-can to trickle irrigation.

The ancient and modern methods of " digging " or " no digging ", " hoeing " or " no hoeing ", are considered by F. A. Bush. The late Eleanor Sinclair Rohde's chapter entitled " Do you dig ?" is most entertaining and encouraging, particularly where she recommends, now that labour is scarce and expensive, that we " rely on Nature's magnificent armies of perfectly trained workers, namely the earthworms which tunnel the soil to a depth of 3 ft., cultivating it as no spade can do . . . ". This is a sobering thought to one who has spent many hours proudly and triumphantly digging with a spade !

The next three chapters are devoted to natural and artificial manures and compost-making, and here the late Sir Albert Howard's methods are fully described.

In his five chapters on propagation, Frank Knight has given an inspiring and meticulous account of the various methods to adopt in the raising of trees and shrubs, herbaceous and rock plants, both vegetatively and from seed. This valuable information is covered by excellent photographs and diagrams. He is obviously speaking from his own practical experience and his detailed descriptions will give confidence and encouragement to all would-be propagators.

No one who has experienced the difficulties of controlling pests and diseases in crops could fail to enjoy the chapters by D. E. Green and the late G. Fox Wilson, and derive great benefit from them. Every aspect of the work is explained, from the most helpful classification of pests and diseases to the many control measures.

Good lawns are the making of a garden and yet so often they are neglected. Mr. Dawson has covered every aspect of treatment from the making of new to the renovation of neglected lawns, and here again is an example of the real expert passing on his knowledge and experience in a really practical manner and in excellent detail.

Perhaps the most outstanding contributions to this most interesting book are those concerning the soil, vegetative propagation, the study of pests and diseases and the management of lawns.

The Editor is to be congratulated on the compilation and organization of this book, as also should be the many authors who have so freely given of their knowledge

and experience. To the many people who are trying to fathom the science and art of growing things in their gardens, this book should be of real value.

B.H.

ABSTRACT BIBLIOGRAPHY OF FRUIT BREEDING AND GENETICS TO 1955. Rubus and Ribes—A Survey. By R. L. Knight and Elizabeth Keep. Technical Commun. No. 25 of the Commonwealth Bureau of Horticulture and Plantation Crops. (Commonwealth Agricultural Bureaux, Central Sales, Farnham Royal, Bucks., England. 1958. Pp. 254. Price 45s.)

The scope of this book is outlined in the Foreword by the authors. It purports to be a survey of literature on Rubus and Ribes published between 1900 and 1955, though a few references to earlier work are also given. Information useful to the plant breeder in the fields of genetics, breeding, and cytology is summarized in detail. Also dealt with are pomological descriptions, classification and synonymy of varieties and species, and their response to insect pests and cryptogamic diseases. In addition gene lists and linkage data, to which the authors themselves have made valuable contributions, are presented in appendices.

No less than 1007 papers have been summarized, and the summaries have been prepared to give the maximum amount of relevant information to workers in these crops. The index is detailed and adequate. The authors have performed a real and lasting service to the whole discipline of applied genetics for, although the aims of the breeder differ materially from crop to crop, information derived from intensive studies in one field may be of great use in others.

What one would like to see, of course, is a great extension of this kind of bibliographical work to other crops. At present, every serious research worker has to prepare his own bibliography, an activity which consumes much time. The number of unpublished and private bibliographies must indeed be very large, and this is to the detriment of plant breeding. May the reviewer hope that the Commonwealth Bureaux will extend their labours to cover more of the important economic crops.

The only thing wrong with this book is the price. Forty-five shillings puts it out of the reach of the individual worker.

S.C.H.

HORTICULTURE IN THE BRITISH COMMONWEALTH. An outline 1958. By D. Akenhead. Technical Commun. No. 26 of the Commonwealth Bureau of Horticulture and Plantation Crops. (Commonwealth Agricultural Bureaux, Central Sales, Farnham Royal, Bucks, England. 1958. Pp. 63. Price 10s.)

In his introduction, the author, who is Director of the Bureau of Horticulture and Plantation Crops, is slightly apologetic because this work concerns only the countries associated with the Commonwealth Agricultural Bureaux. He need not be —for we in the United Kingdom and many outside those countries will be indeed grateful to him for the industry with which he has compressed into its 63 pages a mine of information. All those who have a wide interest in horticulture will find it useful; but to anyone starting on a tour of horticultural stations anywhere in the Commonwealth it will be essential. In it he will find not only where to go, but also a description in brief of what he will see when he gets there. This reviewer only wishes he had had this pocket-sized booklet to refer to a few years ago.

Perhaps, now Mr. Akenhead has given the lead, someone else will compile a similar account of horticultural investigation in other countries. Frankly, we do not envy him the task; but what about starting with the U.S.A.?

T.N.H.

INTENSIVE APPLE CULTURE. Ministry of Agriculture, Fisheries and Food Bulletin No. 49. (London: H.M. Stationery Office. 1958. Pp. 38. illus. Price 4s.)

This bulletin, which has been out of print for nearly 20 years, has now been rewritten in the light of new knowledge acquired during the intervening period. It is written as a guide to growers of high quality fruit on small, closely-planted trees that come into bearing at an early age. It may be considered as complementary to that most valuable bulletin No. 133, *Apples and Pears*.

Three forms of tree are described, " cordons ", " dwarf pyramids " and " dwarf bushes ", these being the forms commonly grown in England, with full details of suitable soils and rootstocks, tree shaping and pruning, soil management and pest and disease control, while nine dessert varieties that might be selected for these forms of culture are described.

A bulletin of this kind must inevitably seem conservative to some, eschewing speculation and only including recommendations that can be made with confidence. Even so, we would warn those who grow dwarf pyramids on M.VII rootstock not to plant them on strong-growing soils, while we should not include Worcester Pearmain, except as a pollinator.

Intensive fruit growers in the United Kingdom will be grateful to the N.A.A.S. Fruit Group for so admirably revising and bringing up to date this bulletin, while others overseas who are now becoming interested in " dwarf trees ", though admittedly their definition of the term may not be the same as ours, may find it profitable reading.

T.N.H.

THE GRAFTERS' HANDBOOK. Second edition. By R. J. GARNER. (London : Faber & Faber. 1958. Pp. 260, illus. Price 25s.)

Few authors of horticultural text-books write with such a wealth and breadth of experience behind them as R. J. Garner, whose long connection with nursery and fruit-farm practice and scientific research makes him our foremost authority on grafting in all its methods and applications.

The first edition of *The Grafter's Handbook*, published in 1946, quickly established itself as a standard work and ran to three impressions. This second edition, although embodying substantially the original text, has been extended considerably in the light of recent research findings and consequent developments in nursery practice.

In addition to the wealth of detail contained in the earlier edition, full information is given on improved methods of commercial tree raising and on labour-saving mechanical aids in tree lifting ; the vital importance of healthy propagating material is emphasized in the light of research into the incidence, spread and control of virus diseases ; the treatment of hardwood cuttings to encourage root initiation before planting will be new to many ; and mist propagation is dealt with very clearly, including a detailed description of the apparatus used.

The many illustrations are clearly and carefully chosen to aid the reader. The

line drawings, executed by the author himself, are obviously by an artist who has himself handled the material being illustrated, and these, together with many excellent photographs, contribute to a clear understanding of the many methods and uses of grafting described.

The author, experienced himself in commercial methods, has produced a book invaluable to the nurseryman ; for the student *The Grafters' Handbook* is an indispensable text-book ; and those who wish for more can turn up the list of 143 references to scientific papers and articles to improve their knowledge further. E.W.H.

NARCISSUS PESTS. Ministry of Agriculture Bulletin No. 51. Fifth edition. (London : H.M. Stationery Office. 1958. Pp. 38, illus. Price 4s. 6d.)

For more than a quarter of a century Hodson's book on narcissus pests, published as Bulletin 51 of the Ministry of Agriculture, has been the only concise and complete work of reference on the subject available in this country. The fifth edition of this bulletin has now been produced by the Plant Pathology Laboratory with the aid of members of the National Agricultural Advisory Service. It follows very closely the previous pattern, with descriptions of the major pests attacking this crop, followed by notes on their life history and the symptoms they produce. The sections on control measures have been brought up to date with somewhat brief descriptions of the use of D.D. for obtaining better growth of narcissus plants in the presence of root-lesion eelworm and of the most important advance in controlling flies by dipping in aldrin or dieldrin. It is now generally agreed that the latter pests have been dealt such a blow by the use of these hydrocarbons, which were investigated and publicized in this country by Woodville, that bulb growers in the South West of England are likely to have many more surplus bulbs for sale than at any time in the past. It would have been better to make shorter mention of the older method of controlling flies and to explain in somewhat greater detail the methods already in large-scale use for dipping in aldrin and dieldrin against these pests.

Ditylenchus dipsaci, which like so many animals and plants has changed its name since early editions, can still be the most devastating pest of this crop. It is serious not only because of the damage and loss it causes, but because of the harm which the only effective control measure can do to stocks of bulbs if timing of the treatment is at all inaccurate. Here the new bulletin has endeavoured to assist by giving a description of the development of the inside of the bulb at the time of hot water treatment, together with a series of diagrams and a statement as to which is the safe period in which to treat the bulbs. Of considerable help also is a description of the method of cutting to find and identify the developing bud. Photographs of this operation and of the developing buds would have been of even greater value.

Several of the other illustrations, like the general pattern of the publication, have stood the test of time and are in general a useful part of the bulletin. There is a bibliography of some length, but it is not easy to identify the new references since the publishers have departed from the established method of printing the authors' names first and in alphabetical order ; they now list them with the title first and in the order in which reference is made in the text.

The bulletin is, however, still much more valuable than its price would suggest and is sure to be useful to advisers, growers and students and, to some extent, to those investigating the problems of the narcissus. F.W.S.

NOTICE TO CONTRIBUTORS

1. All **manuscripts** should be in double-spaced typewriting, with a good margin, and should be addressed to the Editor, East Malling Research Station, near Maidstone, Kent, England. Papers must be written concisely. Historical reviews should be as short as possible and only such references to literature as bear directly on the subject should be included. Tables and illustrations, if any, must be only such as are absolutely essential for clear presentation.

2. Authors of papers containing extensive **numerical observations** should consult the recommendations of the British Association Committee on Biological Measurements, 1927, obtainable from Burlington House, London, W.1, price 6d. Arrangements have been made whereby original data too extensive for complete publication may be deposited at the British Museum (Natural History), London, S.W.7, or with the Royal Society of Edinburgh, 22 George Street, and thus be available for consultation by other workers. Full bibliographical reference to the publication in which the results are summarized must be supplied with the data.

3. Each paper must conclude with a concise and critically correct **summary** of its actual content. It should contain any new or verified constants as well as any other critical data of permanent value but not tables or graphs. Any organism mentioned should be given its scientific name.

4. Where a paper is of a highly technical nature it should be preceded by a brief **synopsis,** in which its contents are simply and clearly stated for the benefit of non-technical readers.

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HORTICULTURAL ABSTRACTS

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